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Faunal distribution and palaeoenvironmental trends in the Lower Ordovician of the Montagne Noire, France: insights into the Cabrières Biota

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In the southern Montagne Noire, France, the upper Floian Cabrières Lagerstätte yielded an atypical and diverse marine assemblage dominated by algae and sponges. It contrasts with the Fezouata Shale, Morocco, the only other known high-latitude Lower Ordovician Lagerstätte where non-trilobite arthropods and echinoderms constitute the two main components of the communities. This paper focuses on the palaeoenvironmental context of the Cabrières Lagerstätte and extends to the entire southern Montagne Noire, where several groups of organisms with high potential for palaeoenvironmental reconstructions, including acritarchs (phytoplankton), as well as numerous echinoderms and trilobites (benthos), combined with sedimentological studies, allow for the analysis of the environmental context of the Cabrières Biota. In the western southern Montagne Noire, the composition of acritarch assemblages recorded from three sections documents an ecological shift from inshore, proximal settings to more distal, open shelf environments. Distinct trilobite and echinoderm assemblages are identified in the Lower Ordovician of the Montagne Noire. Their distribution and taxonomic composition are mainly controlled by depth, as well as possibly by salinity and oxygenation. In most cases, echinoderms were minor components of the diverse benthic communities, often dominated by brachiopods, molluscs, and trilobites. In the Lower Ordovician of the Montagne Noire, echinoderm-dominated assemblages seem to be restricted to unstable, high-energy environments. Trilobites and echinoderms of the Cabrières Biota inhabited soft, poorly-oxygenated substrates in distal and low-energy shelf environments, below the storm wave base. □ *Acritarchs, Cabrières Biota, echinoderms, Montagne Noire, Ordovician, palaeoenvironments.*

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In recent years, the discovery of several Lower Ordovician Konservat-Lagerstätten has significantly contributed to filling the taphonomic gap during a critical transition in the evolution of marine ecosystems, between the so-called Cambrian explosion and the onset of the Great Ordovician Biodiversification Event (e.g. Van Roy *et al.* 2010; Balinski & Sun 2015; Botting *et al.* 2015; Fang *et al.* 2022; Saleh *et al.* 2022, 2024a). While most Cambrian and Lower Ordovician sites with exceptional preservation are restricted to low palaeolatitudes, the Cabrières Lagerstätte (Landeyran Formation; Montagne Noire, France) represents, together with the Fezouata Shale (Anti-Atlas, Morocco), one of the few localities in the world to document high-latitude, fully marine assemblages during the Early Palaeozoic (Saleh *et al.* 2024a). The Cabrières Biota is dominated by algae and sponges (Saleh *et al.* 2024a, 2024b). These two groups are associated with a diverse marine assemblage including arthropods (e.g. ostracods, trilobites; Saleh *et al.* 2024a), brachiopods (Harper *et al.* this volume), cnidarians (conulariids, *Sphenothallus*; Van Iten *et al.* this volume), graptolites (Gutiérrez-Marco *et al.* this volume), hyolithids, molluscs (e.g. bivalves, cephalopods, gastropods, rostroconchs; Polechová *et al.* this volume), various vermiform organisms (Vannier *et al.* this volume), and trace fossils (Gougeon *et al.* this volume), among other groups.

Although the Cabrières and Fezouata biotas share many similarities in terms of faunal composition, associated environmental conditions, and taphonomic processes, they also exhibit significant differences. For example, two of the dominant and most salient components of the Fezouata assemblages, non-trilobite arthropods (e.g. aglaspidids, marrellomorphs, radiodonts, xiphosurans) and echinoderms (e.g. eocrinoids, solutans, somasteroids, stylophorans), are particularly rare in the Cabrières Biota (Saleh *et al.* 2024a, 2024b). In the Cabrières Lagerstätte, the preservation of non-biomineralized algae (Vayda *et al.* this volume) and particularly delicate, lightly skeletonized sponges (Li & Reitner this volume) suggests that the rarity of non-arthropod trilobites and echinoderms is probably not the result of a taphonomic bias, but rather of differences in palaeoenvironmental conditions. Reconstructing the original environmental context in which the organisms once lived and deciphering the complex taphonomic pathways leading to their exceptional preservation is a particularly challenging task, requiring the integration of data from different fields (geochemistry, ichnology, palaeontology, and sedimentology) (Saleh *et al.* in press).

The first objective of this study is therefore to contribute to elucidating the palaeoenvironmental context of the Cabrières Biota through the detailed analysis of organisms originally occupying different ecological niches, being part of the phytoplankton (acritarchs) and the benthos (echinoderms and trilobites). In the Lower Ordovician of the western part of the southern Montagne Noire, where sections are better exposed, the evolution of acritarch, echinoderm and trilobite assemblages in coeval levels of the lower part of the Landeyran Formation, combined with sedimentological data (Vaucher *et al.* this volume), trace fossils (Gougeon *et al.* this volume), and results obtained from other taxonomic groups (e.g. Harper *et al.* this volume, Polechová *et al.* this volume, Van Iten *et al.* this volume), provide crucial new information on the palaeoenvironmental conditions associated with the Cabrières Biota. The second objective of this paper is to analyse the evolution of benthic communities (echinoderms and trilobites) from the southern Montagne Noire over a broader time scale (late Tremadocian–late Floian), to better unravel the likely influence of the different environmental parameters (e.g. bathymetry, oxygenation, salinity) on their distribution.

Geological context

The southern Montagne Noire is a geologically complex area (Fig. 1). Its structure of folded units (nappes) is inherited from the Variscan orogeny (Gèze 1949; Demange 1998, 1999, 2001; Franke *et al.* 2011; Chardon *et al.* 2015, 2020). However, relatively comparable Cambrian-Ordovician successions, characterized by similar facies and faunas, have been identified in most tectonic units (Minervois, Pardailhan, Mont Peyroux, Faugères, and Pic de Vissou units; Fig. 1), suggesting that they were originally part of the same palaeogeographical area, on the passive margin of Gondwana (Vizcaïno *et al.* 2001; Lefebvre *et al.* 2023). At the northeastern extremity of the southern Montagne Noire, markedly different Ordovician successions have been described in the Cabrières unit (Fig. 1; Fournet 1850; Graff 1874; de Rouville & Delage 1892; Miquel 1894, 1912; Thoral 1941, 1946; Álvaro *et al.* 2016). In this area, Ordovician deposits are embedded as olistoliths in Carboniferous wildflysh (Gèze 1949; Feist & Echtler 1994; Demange 2001; Aretz 2016; Chardon *et al.* 2020). The Cabrières unit differs from other units of the southern Montagne Noire not only by its tectonic style, but also by its sedimentary succession and faunas. In the Cabrières unit, Cambrian deposits are absent, the Lower Ordovician faunas and successions are difficult to correlate with those of the other units. Finally, this region has yielded abundant and diverse Late Ordovician assemblages, absent elsewhere in the Montagne Noire, but suggesting affinities with the Mouthoumet Massif (Corbières) and the Pyrénées (Touzeau *et al.* 2012; Colmenar *et al.* 2013; Álvaro *et al.* 2016, 2018; Lefebvre *et al.* 2023).

In the Minervois, Pardailhan, and Mont Peyroux units, the ~2,000-metre-thick Lower Ordovician succession has been subdivided into six lithostratigraphical units: from bottom to top, the La Dentelle, Saint-Chinian, La Maurerie, Cluse de l'Orb, Foulon, and Landeyran formations (Fig. 2; Capéra *et al.* 1978; Courtessole *et al.* 1981, 1983; Vizcaïno *et al.* 2001; Lefebvre *et al.* 2023). The lower part of this succession

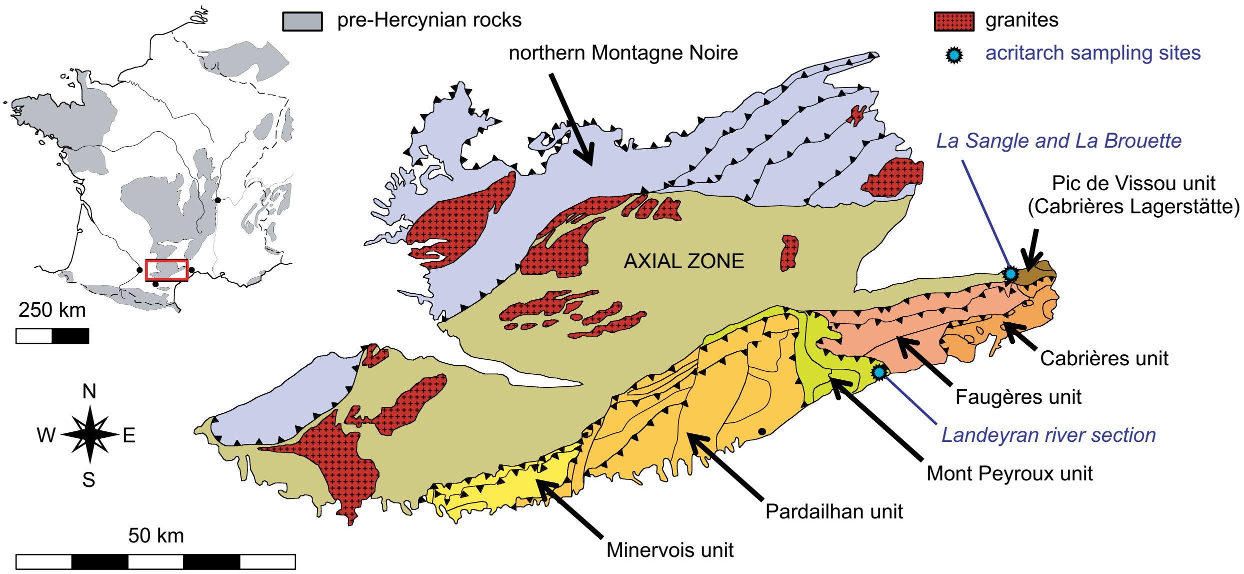
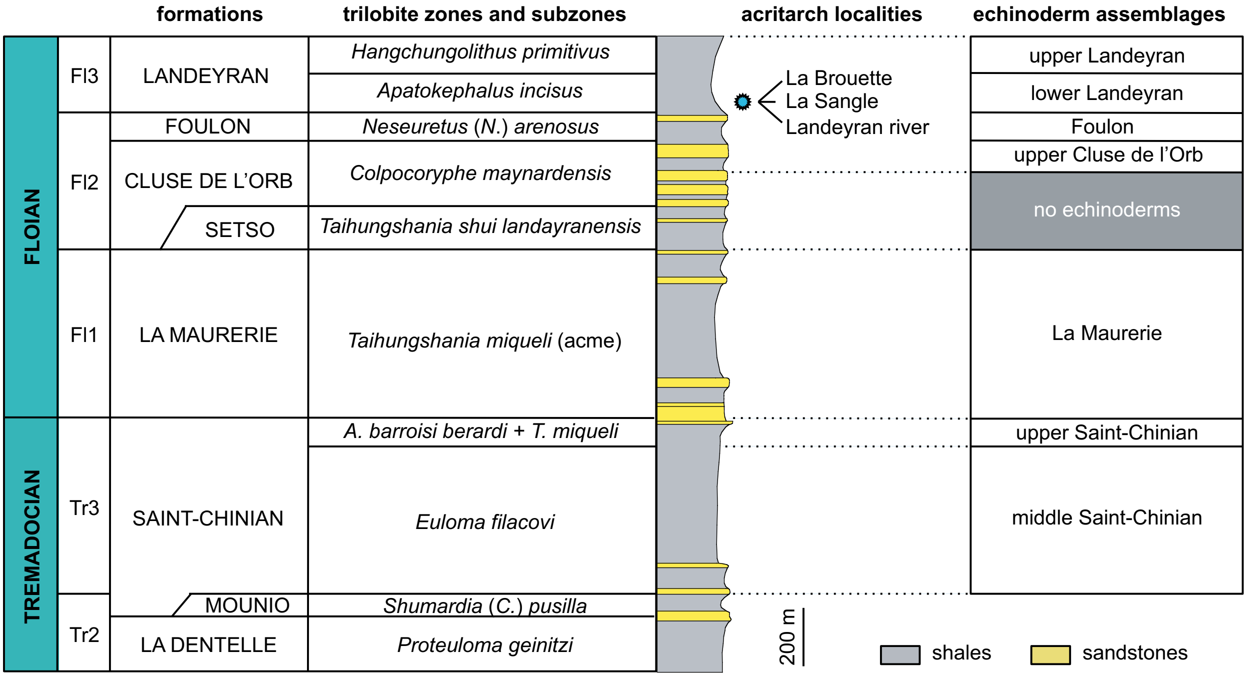


Fig. 1. Location of the Montagne Noire at the southern extremity of the French Massif Central, and simplified geological map of the Montagne Noire, showing the main tectonostratigraphical units of the southern side, as well as the three sampling sites for acritarchs. Redrawn and modified after Demange (1999).



		formations	trilobite zones and subzones	acritarch localities	echinoderm assemblages
FLOIAN	Fl3	LANDEYRAN	*Hangchungolithus primitivus*		upper Landeyran
			Apatokephalus incisus	La Brouette La Sangle Landeyran river	lower Landeyran
	Fl2	FOULON	*Neseuretus (N.) arenosus*		Foulon
		CLUSE DE L'ORB	*Colpocoryphe maynardensis*		upper Cluse de l'Orb no echinoderms
		SETSO	*Taihungshania shui landayranensis*		no echinoderms
	Fl1	LA MAURERIE	*Taihungshania miqueli* (acme)		La Maurerie
TREMADOCIAN	Tr3	SAINT-CHINIAN	*A. barroisi berardi + T. miqueli*		upper Saint-Chinian
			Euloma filacovi		middle Saint-Chinian
		MOUNIO	*Shumardia (C.) pusilla*		
	Tr2	LA DENTELLE	*Proteuloma geinitzi*		

Fig. 2. Lower Ordovician stratigraphical framework of the southern Montagne Noire with lithostratigraphical units, trilobite biozonation, synthetic log, stratigraphical position of the sampling sites for acritarchs, and of the six successive echinoderm assemblages identified herein. Redrawn and modified from Courtessole *et al.* (1981) and Vizcaïno & Álvaro (2003).

exhibits a general regressive trend from the moderately deep, offshore to open shelf shales of the Saint-Chinian Formation to the shallower, thick sandstone deposits of the Cluse de l'Orb Formation recording a wave-influenced delta flanked by shoreface environments (Vaucher *et al.* this volume). The upper part of the succession documents a well-defined transgressive trend, culminating in the lower part of the Landeyran Formation (Dean 1966; Courtessole *et al.* 1991; Vizcaïno *et al.* 2001; Lefebvre *et al.* 2023; Gougeon *et al.* this volume; Vaucher *et al.* this volume). Biostratigraphy of the Lower Ordovician succession in the southern Montagne Noire (Fig. 2) is based mainly on trilobites, with minor contributions based on agnostids and conodonts (Dean 1966; Capéra *et al.* 1978; Courtessole *et al.* 1981, 1983; Vizcaïno *et al.* 2001; Vizcaïno & Álvaro 2003; Tortello *et al.* 2006; Serpagli *et al.* 2007; Lefebvre *et al.* 2023).

The Cabrières Lagerstätte has been described from several sites, all situated in the Pic de Vissou unit (Fig. 1; Saleh *et al.* 2024a). Therefore, the acritarch, echinoderm, and trilobite assemblages of the Cabrières Biota will be primarily compared with documented occurrences of these taxa in the Minervois, Pardailhan and Mont Peyroux units. Based on their lithology and faunal content (acritarchs, graptolites, trilobites), the strata providing the Cabrières Biota can be correlated with the lowermost part of the Landeyran Formation (Saleh *et al.* 2024a; Caillaud *et al.* this volume; Gutiérrez-Marco *et al.* this volume). In terms of biostratigraphy, these levels correspond to the base of the *Apatokephalus incisus* trilobite Zone (late Floian; Fig. 2). Echinoderm and trilobite remains and acritarch assemblages have also been mentioned several times from the Cabrières unit (see e.g. Miquel 1912; Thoral 1946; Rauscher 1971, 1974; Martin 1972; Capéra *et al.* 1978). However, they will not be considered here for comparison, because their fossil content is more closely related to the Corbières and Pyrénées than to the other units of the Montagne Noire.

Material and methods

This study focuses on three taxonomic groups of the Cabrières Biota. However, they are not analysed here in exactly the same localities and levels. The analyses of the acritarch assemblages are exclusively based on data from the Landeyran valley section in the Mont Peyroux unit (i.e. the upper part of the Foulon Formation and the base of the overlying Landeyran Formation) and the Cabrières area (lower part of the Landeyran Formation). Regarding echinoderms and trilobites, the material collected over the past 150 years enables the analysis of the entire succession from the Saint-Chinian to Landeyran formations (Fig. 2).

Acritarchs

In 2024, three localities were sampled for palynomorphs in the Floian succession of the southern Montagne Noire (Caillaud *et al.* this volume). The Landeyran river section (Vaucher *et al.* this volume) corresponds to the classic locality regularly mentioned as 'Upper Bridge' (sites λ1, λ2, and λ3; Dean 1966) or 'Pont Supérieur' in the literature (e.g. Courtessole *et al.* 1981, 1983; Ubaghs 1991; Lefebvre & Vizcaïno 1999). This section is located on the west bank of the Landeyran river, in the Landeyran valley, and on the territory of the Saint-Nazaire-de-Ladarez municipality (Hérault; Fig. 1). Located in the Mont Peyroux unit, the Landeyran river locality provides a nearly continuous 105-metre-thick section exposing the transition between the almost vertical, uppermost beds of the Foulon Formation and the lowermost part of the overlying Landeyran Formation (Dean 1966; Gougeon *et al.* this volume; Vaucher *et al.* this volume). Sixteen rock samples for palynological analysis were collected at regular intervals from the shales of the Landeyran river section (Fig. 3; Caillaud *et al.* this volume).

Acritarchs were also sampled in two other localities ('La Brouette' and 'La Sangle', Cabrières municipality), both situated in the Pic de Vissou unit (Fig. 1) and yielding typical assemblages of the Cabrières Biota (Saleh *et al.* 2024a; Caillaud *et al.* this volume). At these two sites, detailed sections could not be logged because of the limited exposure and complex local geological setting (faults). However, the composition of both the acritarch assemblages (Caillaud *et al.* this volume) and the associated fauna (graptolites, trilobites; Saleh *et al.* 2024a; Gutiérrez-Marco *et al.* this volume), support the attribution of the two localities of La Brouette and La Sangle to the lowermost part of the Landeyran Formation, i.e. to levels more or less coeval with those exposed along the Landeyran river section (Fig. 3).

The precise methodology used for acritarch preparation (extraction, sieving), observation and identification has been fully described in Caillaud *et al.* (this volume). It will therefore not be repeated here. All prepared samples and corresponding palynological slides are deposited in the palaeontological collections of Lille University.

Echinoderms and trilobites

Most of the echinoderm and trilobite specimens from the Pic de Vissou unit were collected from the same two localities as those yielding the acritarchs (La Brouette and La Sangle), as well as from a third nearby site (La Bâche), also providing assemblages typical of the Cabrières Biota (lowermost part of the Landeyran Formation). In 2024, additional material (mostly echinoderms) was also collected from

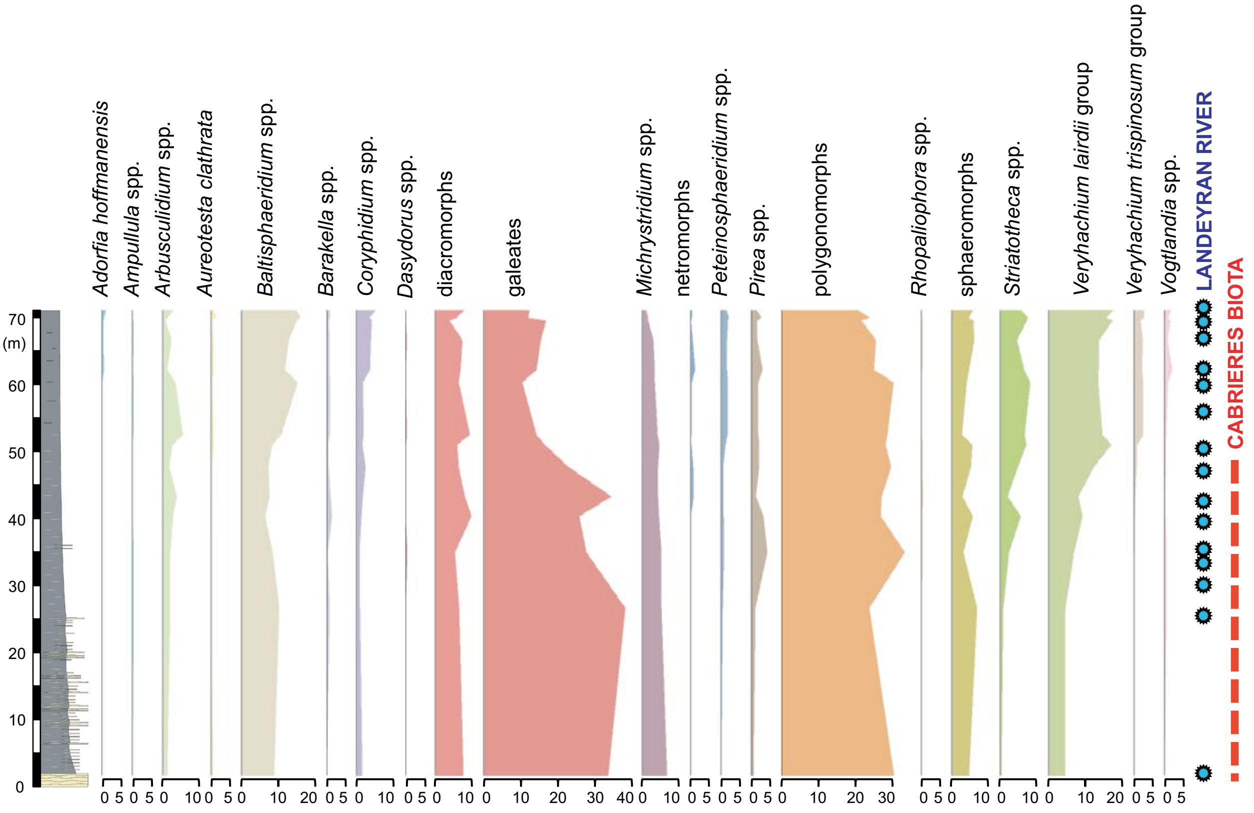


Fig. 3. Variation in the abundance of late Floian acritarchs collected at the Landeyran river section (Saint-Nazaire-de-Ladarez, Montpeyroux unit, southern Montagne Noire), immediately above the contact between the Foulon and Landeyran formations. The precise stratigraphical position of each level sampled for acritarchs at the Landeyran river locality is reported on the log, as well as the stratigraphical interval estimated for the Cabrières Biota, based on the composition of acritarch assemblages collected at the two sites of La Brouette and La Sangle (Cabrières area, Pic de Vissou unit). Log of the Landeyran river section modified from Vaucher *et al.* (this volume).

a nearby locality situated on the territory of the municipality of Mourèze (Hérault), yielding slightly older assemblages from the uppermost part of the Foulon Formation. All studied echinoderms and trilobites from the Pic de Vissou unit are deposited in the collections of the Cabrières municipality (UCBL-CAB34) and in the palaeontological collections of the Université Claude Bernard Lyon 1 (UCBL-FSL).

Echinoderm and trilobite specimens are preserved as moulds in the rock. Their identification, therefore, often requires a latex cast to recreate their original, three-dimensional appearance. All figured samples were coated with ammonium chloride (NH_4Cl), and photographed with a Canon 5DSR camera equipped with a MP-E 65 or 100 mm macro lens. The number of trilobites collected in the Cabrières region is relatively small (54 specimens). The pygidium and the cranidium (when more than 50% preserved), as well as the thoracopygidium, the hypostome, or the cephalothorax were counted as separate individuals, which could overestimate the number of specimens potentially preserved as separate cephalic and pygidial fragments. Even when recognizable, the cheeks and thorax were not included in the count.

A dataset gathering all the echinoderm specimens from the Lower Ordovician of the Minervois, Pardailhan and Mont Peyroux units registered in the main public palaeontological collections was constructed to analyse the sampling effort in the southern Montagne Noire over the past 150 years, and also to better estimate their diversity and abundance in the five most sampled lithological units (Saint-Chinian, La Maurerie, Cluse de l'Orb, Foulon, and Landeyran formations). All echinoderm specimens were assigned to seven stratigraphical intervals (Fig. 2). The dataset is available online (https://osf.io/g8yhw/) and includes 996 specimens deposited in the following public institutions: Géosciences Rennes (IGR), Musée du Biterrois, Béziers (MB), Muséum d'Histoire Naturelle de Toulouse (MHNT), Muséum National d'Histoire Naturelle (MNHN), Université Claude Bernard Lyon 1 (UCBL-FSL), and Université de Montpellier (UM).

Compositional differences among echinoderm assemblages were investigated using Bray-Curtis dissimilarities computed from the echinoderm dataset, through a hierarchical clustering and a non-metric multidimensional scaling (NMDS) ordination. Influence of environmental parameters (such as the oxygenation level and the depositional environment) on echinoderm communities was tested using PERMANOVA, complemented with both Indicator Species analysis and SIMPER (see the supplementary material for further details). All analyses were conducted in R using the packages *ape*, *clustsig*, *indicspecies, pvclust*, and *vegan* (Clarke *et al.* 2008; De Cáceres & Legendre 2009; Paradis & Schliep 2019; Suzuki *et al.* 2019; Oksanen *et al.* 2025; R Core Team 2025).

Considering the trilobites, collected over the same period, the material has been mostly deposited at the Université de Montpellier (UM) and at the Université Claude Bernard Lyon 1 (UCBL-FSL). In the absence of a database on trilobites, the analysis of this group from the Lower Ordovician of the Minervois, Pardailhan and Mont Peyroux units, is based primarily on previous publications (e.g. Dean 1966; Courtessole *et al.* 1981, 1983, 1985, 1991; Capera *et al.* 1978; Pillet 1988; Dolambi & Gond 1992; Vidal 1996a; Vizcaïno *et al.* 2001; Vizcaïno & Álvaro 2003). Since the 1980s, stratigraphical subdivisions have been based on trilobite occurrences allowing the establishment of successive 'faunizones' which cover all the Ordovician lithological units (Saint-Chinian, La Maurerie, Cluse de l'Orb, Foulon, and Landeyran formations).

Acritarch, echinoderm and trilobite assemblages from the Cabrières Biota and their palaeoenvironmental control

Acritarchs

Results. – At the Landeyran river section, all levels sampled in the lower part of the Landeyran Formation yielded abundant acritarch remains (Fig. 3; Caillaud *et al.* this volume). The assemblage is particularly diverse and dominated by galeates (*Caldariola*, *Cymatiogalea*, *Priscogalea*, *Stelliferidium*) and polygonomorphs (e.g. *Polygonium*). Other significant groups include baltisphaerids (*Baltisphaeridium* spp.), diacromorphs (e.g. *Acanthodiacrodium*, *Arbusculidium*, *Barakella*), sphaeromorphs (e.g. *Leiosphaerida*), striated rectangular-shaped taxa attributed to *Striatotheca*, and veryhachids (*Veryhachium lairdii* and *V. trispinosum* groups). Other, less common taxa include *Adorfia*, *Ampullula*, *Aureotesta*, *Coryphidium*, *Dasydorus*, *Micrhystridium*, netromorphs, *Peteinosphaeridium*, *Pirea*, *Rhopaliophora*, and *Vogtlandia* (Fig. 3). Some taxa are age-diagnostic, providing a precise biostratigraphical framework (Caillaud *et al.* this volume). In addition, some taxa present in the assemblages are typical of the high-latitude peri-Gondwana acritarch province (Caillaud *et al.* this volume).

More interestingly for palaeoenvironmental considerations, the varying proportions of acritarch morphotypes clearly allow palaeoecological interpretations, because some taxa only occur in shallow water environments (sometimes related to fresh or brackish water settings). Although some taxa do not show significant variation in their abundance across the section (e.g. most diacromorphs, netromorphs, polygonomorphs, sphaeromorphs), two opposite trends can be highlighted in other groups (see Fig. 3). Some taxa (galeate acritarchs and *Michrystridium*) are more abundant in the lower part of the section, but represent only a minor component of the assemblages in the upper part. Conversely, other taxa (*Arbusculidium*, *Baltisphaeridium*, *Coryphidium*, *Peteinosphaeridium, Striatotheca*, members of the *Veryhachium lairdii* group, and *Vogtlandia*) contribute very little to the assemblages in the lower part of the section, but display higher abundances in the upper part.

In the Cabrières area, variations through time in the abundance of acritarchs could not be documented due to the limited exposure and complex local geological setting. However, the two samples from the Pic de Vissou unit were also fossiliferous and yielded the same acritarch assemblage as in the Landeyran river section (Caillaud *et al.* this volume). Based on the proportions of the different acritarch groups, a tentative correlation can be established between the Landeyran river section and the two localities from the Cabrières area. While the abundance of *Baltisphaeridium* in the two Cabrières samples is reminiscent of the situation at the top of the Landeyran river section, the proportions of galeates and of the *Veryhachium lairdii* group are closer to those observed in the lower part of the Landeyran river section (Fig. 3).

Discussion. – In modern oceans, phytoplankton distribution is strongly influenced by several environmental parameters (e.g. bottom water oxygenation, light, nutrient availability, salinity, sea-surface temperature), and this was probably also true during the early Palaeozoic. Variations in the composition of acritarch assemblages have therefore been widely used by palaeopalynologists for palaeoenvironmental reconstructions, and especially, as a proxy to evaluate the distance to the shoreline (see e.g. Staplin 1961; Riegel 1974; Jacobson 1979; Colbath 1980; Dorning 1981, 1987; Dorning & Bell 1987; Xu 1997; Vecoli 2000;

Li *et al.* 2004; Molyneux 2009; Yan & Li 2010; Yan *et al.* 2013). For example, several studies have demonstrated that smooth-walled acritarchs (e.g. netromorphs, sphaeromorphs) were more abundant in shallow environments, while the proportion of highly ornamented taxa with more complex, stronger and longer processes (e.g. *Ampullula*, *Baltisphaeridium*, *Peteinosphaeridium*, *Rhopaliophora*, *Veryhachium*, *Vogtlandia*) increased with water depth (Staplin 1961; Riegel 1974; Servais *et al.* 2004; Stricanne *et al.* 2004; Calero-Gordon *et al.* 2025). Palaeoecological models of Ordovician acritarch distribution have identified successive assemblages, based on the relative proportions and abundance of taxa: nearshore settings are generally dominated by netromorphs and sphaeromorphs; offshore, open marine environments are characterized by higher diversity assemblages comprising baltisphaerids, michrystrids, *Polygonium*, and veryhachids; finally, highly ornamented forms are dominant in the more distal, outer shelf settings (see e.g. Jacobson 1979; Xu 1997; Vecoli 2000; Li *et al.* 2004; Calero-Gordon *et al.* 2025).

In the Landeyran river section, taxa generally considered as proxies for nearshore settings (i.e. netromorphs and sphaeromorphs) are present, but they constitute minor components (Fig. 3). It becomes immediately evident that these acritarch assemblages were not deposited in a shallow-water environment. However, the assemblages are clearly dominated by the galeates and polygonomorphs, with decreasing proportions for both groups. On the other hand, the increasing proportion of baltisphaerids, together with the mere presence of taxa with complex processes (e.g. *Adorfia*, *Peteinosphaeridium*, *Vogtlandia*), clearly suggest a transition to more distal environmental conditions. Also of interest is a clear increase in the proportion of the *Veryhachium lairdii* group and *Coryphidium* species.

The acritarch assemblages of the Landeyran river section therefore clearly do not exhibit nearshore, shallow-water environments, but a transition from an inner shelf environment (dominance of *Polygonium* and galeates, rare sphaeromorphs and netromorphs) to more distal settings (gradual decrease of galeates and michrystrids, increasing proportions of *Baltisphaeridium* and *Peteinosphaeridium*, and presence of taxa with complex process morphologies, that are usually only found in open shelf environments). The transgressive trend suggested by acritarch assemblages at the base of the Landeyran Formation agrees well with ichnological and sedimentological data, both indicating a similar evolution towards more distal environmental conditions (Gougeon *et al.* this volume; Vaucher *et al.* this volume).

Trilobites

Results. – Over the past six years, 54 trilobites and trilobite fragments have been collected from the lower part of the Landeyran Formation in the Cabrières area (Pic de Vissou unit). They appear as isolated cephalon, pygidium, hypostome, or more or less damaged articulated carapaces (Fig. 4).

The material comes mainly from the La Brouette locality (45 specimens) and, to a lesser extent, from La Sangle (9 specimens). The third locality (La Bâche) also yielded some trilobite specimens (Eric and Sylvie Monceret, pers. obs. 2025), with similar taxa to those of the other two localities; however, as they have not yet been deposited in a public collection, they were not included in the study. At La Brouette, the 45 specimens comprise six cranidia, four cephalons, 12 isolated pygidia, two hypostomes, one incomplete thorax and 20 partial to complete articulated exoskeletons (i.e. cephalothorax, thoracopygidium or exoskeleton). Despite the poor preservation of many specimens, the proportionally high number of articulated exoskeleton parts supports a likely autochthonous origin of the fossilized organisms, which were not transported previously to burial.

The trilobites are mainly preserved as external or internal molds; no antennae, appendages or internal parts have been identified so far, which is a significant difference from exceptionally preserved trilobites from the Fezouata Shale (Saleh *et al.* 2021a, 2022). The La Brouette locality yielded the most diverse trilobite assemblage, dominated by Asaphidae (mainly *Asaphellus,* probably *Merlinia*: 22 specimens; Fig. 4H–J), and Raphiophoridae with *Ampyx* (8 specimens; Fig. 4C). In addition to these dominant taxa, the La Brouette trilobite assemblage comprises *Colpocoryphe* (3 specimens; Fig. 4A), *Taihungshania* (1 specimen; Fig. 4D–E), *Parabathycheilus* (1 specimen; Fig. 4B), *Geragnostus* (2 specimens; Fig. 4G), *Selenopeltis* (1 damaged thorax), and *Apatokephalus* (1 specimen; Fig. 4F). Among these specimens, some individuals can be identified at species level (e.g. *Colpocoryphe thorali*, *Geragnostus boutouryensis*), but in general, tectonic distortion and flattening made species assignment difficult. Besides these taxa, one specimen may belong to the family Nileidae, but more material is needed for an accurate analysis.

La Sangle yielded nine specimens, all attributed to asaphids when their state of preservation allows them to be identified. Among this material, several pygidia are wrinkled with very little or no relief (Fig. 4J). These specimens suggest a peculiar preservation (wrinkled and flattened) possibly corresponding to fresh moults (Drage & Daley 2016; Drage *et al.* 2019;

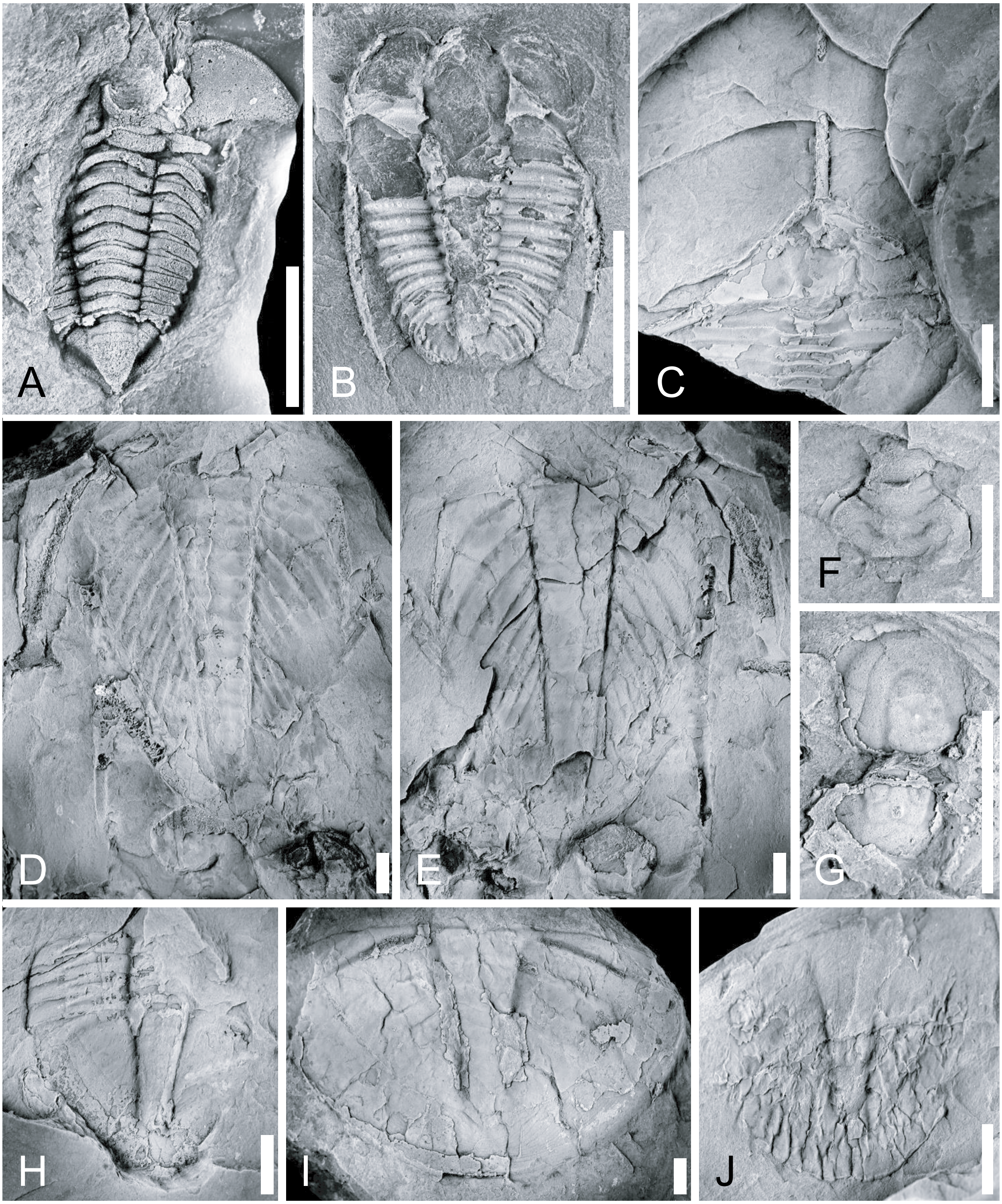


Fig. 4. Trilobites from the Cabrières Biota, lower part of the Landeyran Formation (*A. incisus Zone*, late Floian), Cabrières, Pic de Vissou unit, southern Montagne Noire. A, *Colpocoryphe thorali*, UCBL-CAB34 356 (latex cast). B, *Parabathycheilus* sp., UCBL-FSL 717860 (internal mould). C, *Ampyx* sp., UCBL-FSL 713598 (external mould). D, E, *Taihungshania* sp., UCBL-FSL 717854. D, internal mould. E, external mould. F, *Apatokephalus* sp., UCBL-FSL 714078 (internal mould of the glabella); G, *Geragnostus boutouryensis*, UCBL-FSL 713865 (internal mould). H, *Merlinia*? sp., UCBL-FSL 713863 (internal mould). I, *Asaphellus* sp., UCBL-FSL 717832 (internal mould). J, wrinkled pygidium of Asaphidae, UCBL-FSL 717835 (internal mould). All scale bars: 5 mm.

Daley *et al.* this volume). Preservation effects due to compressive tectonics cannot be excluded in this locality and a more detailed study is necessary with more material to better distinguish hard, well mineralized, exoskeletons from putatively fresh moults.

Discussion. – Unlike the numerous trilobites collected in the Minervois, Pardailhan and Mont Peyroux units (Vizcaïno *et al.* 2001) presenting a high diversity with about 40 genera along the Ordovician succession, the trilobites from the Pic de Vissou unit have a low generic diversity, with nine taxa identified so far. Nevertheless, considering the whole Landeyran Formation, about 15 genera for more than 30 species have been described in the southern Montagne Noire and the Landeyran valley (Vizcaïno *et al.* 2001). As for echinoderms (see below), the sampling effort is not comparable between the Landeyran valley and the Cabrières area; the diversity of trilobites of the Cabrières Biota will probably increase in the future.

In the southern Montagne Noire, the stratigraphical range of *Apatokephalus*, *Colpocoryphe thorali* and *Geragnostus boutouryensis* is restricted to the lower part of the Landeyran Formation (*Apatokephalus incisus* Zone) (Dean 1966; Courtessole *et al.* 1991; Tortello *et al.* 2006). Therefore, the presence of these three taxa in the Cabrières Biota corroborates the age and correlations based on acritarchs and graptolites (see e.g. Caillaud *et al.* this volume).

During the Ordovician, trilobites exhibited maximum morphological disparity depending on their environment and life habits, allowing biofacies to be described along a proximal-distal transect (see Fortey & Owens 1978, 1987, 1997; Vaněk 1995; Zhiyi *et al.* 2003; Mergl *et al.* 2008; Owen & Romano 2011; Zhou *et al.* 2011). In the Cabrières Biota, the relative abundance of Asaphidae and Raphiophoridae corresponds to the raphiophorid biofacies, originally described by Fortey and Owens (1978). Combined faunal and sedimentological analyses in the Fezouata Shale (Morocco) have clarified the environment of this raphiophorid assemblage in the offshore, on both sides of the storm wave base (Vidal 1996b; Martin *et al.* 2016; Vaucher *et al.* 2016, 2017). No typical pelagic or atheloptic trilobites, representative of outer shelf platform to oceanic environments, have been identified so far in the Cabrières Biota. Despite a small number of specimens, the typical and very homogeneous assemblage of the raphiophorid biofacies in Cabrières suggests a local origin and their autochthonous burial without mixing due to transport as already proposed by the articulated remains.

The absence of soft tissue in the trilobites from the Cabrieres Biota must be put into perspective. The Cabrières Biota was described only recently, unlike the Fezouata Biota, which was discovered more than twenty years ago. Despite this, thousands of trilobites have been found in the Fezouata Biota, but only a few dozen have soft-tissues or weakly mineralized remains. For example, in the Marrakesh collections, which systematically include most of the Fezouata fossils found during fieldwork, regardless of their state of preservation, more than 600 trilobites are inventoried, of which only a dozen preserve soft tissues. It is therefore not unlikely that, in the future, soft-tissues will be discovered in trilobites from the Cabrières Biota.

Echinoderms

Results. – Over the past six years (2018–2024), relatively intensive sampling at the three main localities of the Cabrières Lagerstätte (La Bâche, La Brouette and La Sangle) has yielded around 20 specimens of relatively small-sized echinoderms. This assemblage, which includes at least six different taxa, is dominated by the glyptocystitid rhombiferan *Macrocystella* sp. (Fig. 5A) and two eocrinoids: *Balantiocystis* sp. (Fig. 5B) and a yet undescribed rhipidocystid (Fig. 5C). The Cabrières assemblage also comprises the two cornutes *Nanocarpus dolambii* (Fig. 5E) and *Thoralicystis*? *ubaghsi*, as well as the mitrate *Ovocarpus moncereti* (Fig. 5D).

The echinoderms from the Cabrières Lagerstätte show a wide range of preservation. Several specimens of *Balantiocystis* and *Macrocystella* consist of fully articulated individuals, in which not only the theca is preserved, but also very delicate skeletal structures, such as the feeding appendages (brachioles) and the stem (Fig. 5A, B). The same is true for stylophorans, many of which consist of fully articulated individuals, with their aulacophore preserved and inserted in the theca (Fig. 5E). In some other individuals, the appendages (aulacophore, brachioles, stem) are absent and only the theca, partly disarticulated and collapsed, is preserved (Fig. 5D). Finally, remains of totally disarticulated echinoderms are also present. Some of these can be easily assigned to a specific taxon (e.g. the large thecal plates and ring-like proximal columnals of *Macrocystella*), while others are more difficult to identify. Skeletal fragments may be isolated or occur as small clusters of disarticulated echinoderm plates. In the same nappe as the Cabrières Lagerstätte (Pic de Vissou unit; Fig. 1), an excavation in the nearby locality of Mourèze in the stratigraphically slightly older deposits of the Foulon Formation yielded hundreds of isolated echinoderm skeletal elements (mostly columnals), all probably belonging to eocrinoids (*Lingulocystis* spp.).

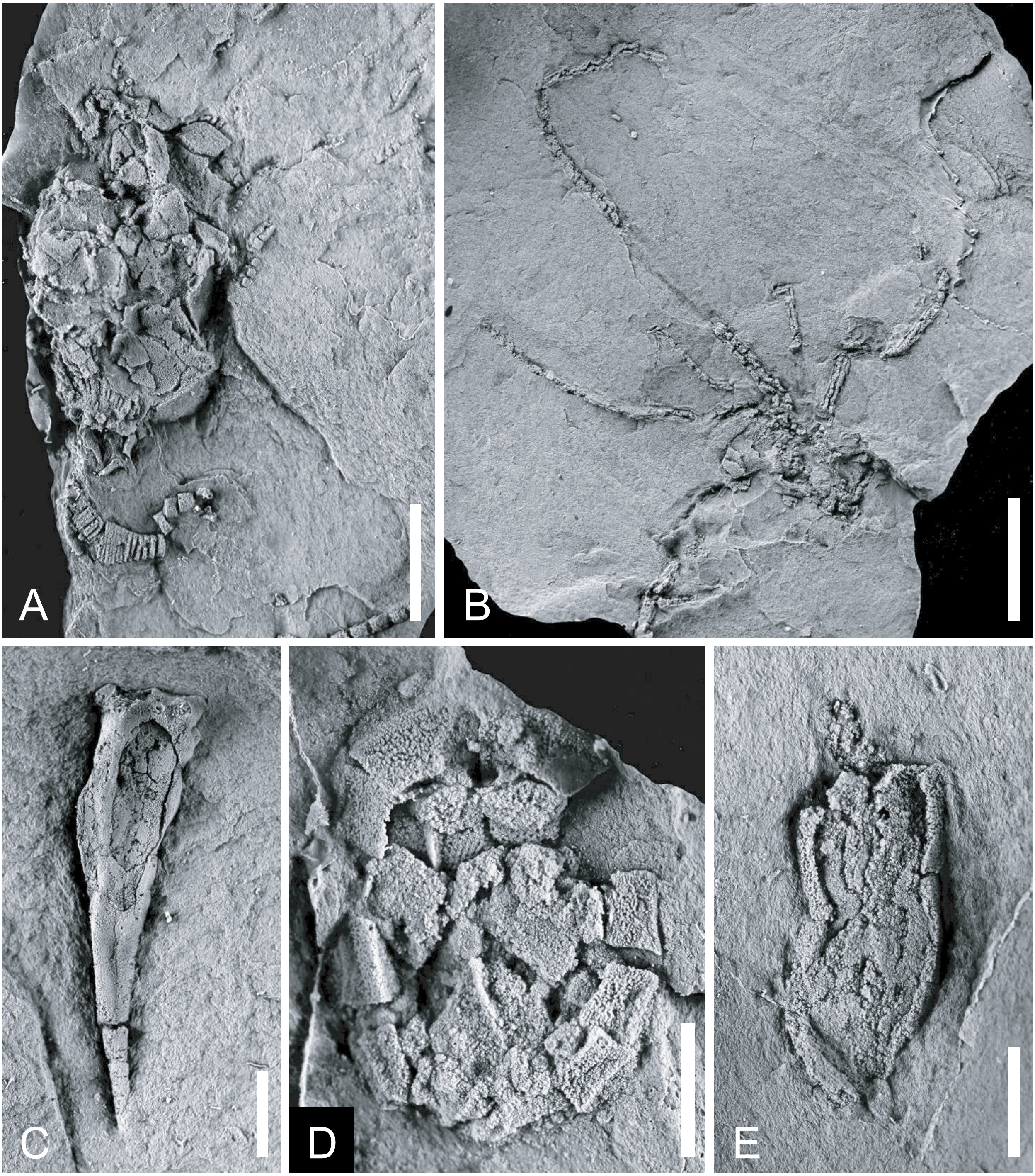


Fig. 5. Echinoderms from the Cabrières Biota, lower part of the Landeyran Formation (*A. incisus Zone*, late Floian), Cabrières, Pic de Vissou unit, southern Montagne Noire. A, *Macrocystella* sp. (Glyptocystitida): complete theca, with brachioles and partly disarticulated stem, UCBL-FSL 717 884. B, *Balantiocystis* sp. (Eocrinoidea): oral surface of theca with articulated brachioles, UCBL-FSL 713 639. C, rhipidocystid indet. (Eocrinoidea): fully articulated theca and proximal part of the stem, UCBL-FSL 713 721. D, *Ovocarpus moncereti* (Mitrata): partly collapsed theca in upper aspect; aulacophore missing, UCBL-FSL 713 596. E, *Nanocarpus dolambii* (Cornuta): complete, slightly disarticulated theca and proximal aulacophore, in lower aspect, UCBL-FSL 718 466. Scale bars: 5 mm (A, B), 2 mm (C–E).

Discussion. – Taphonomic experiments on extant echinoderm taxa have shown that within one or two weeks after death, the multi-element endoskeleton of echinoderms completely disarticulates into hundreds to thousands of individual skeletal elements, once the mesodermal soft tissues (muscles, ligaments) that bind them together during life have decayed (Donovan 1991; Nebelsick 1995, 2004; Brett *et al.* 1997; Ausich 2001; Thompson *et al.* 2025). Preservation of fully articulated individuals and especially of their most fragile parts (e.g. aulacophore, brachioles) therefore requires their rapid burial by obrution deposits (Brett *et al.* 1997; Ausich 2001; Martin *et al.* 2015; Nardin & Régnault 2015; Lefebvre *et al.* 2022a; Saleh *et al.* 2023).

In the Cabrières Lagerstätte, the exceptional preservation of several fully articulated specimens of *Balantiocystis* and *Macrocystella* (with their brachioles, stem and theca; Fig. 5A, B) implies that they were buried alive or very soon after death, as is the case in most 'echinoderm Lagerstätten' (see e.g. Smith 1988; Brett *et al.* 1997; Ausich 2001; Lefebvre *et al.* 2016; Cole *et al.* 2018; Saleh *et al.* 2023; Fatka *et al.* 2025). In the same levels, the presence of partly disarticulated thecae and isolated skeletal elements suggests that obrution deposits also buried already dead and decaying echinoderms (Brett *et al.* 1997; Saleh *et al.* 2023). In the Cabrières Lagerstätte, the occurrence of fully articulated echinoderms as well as decaying and collapsed carcasses is consistent with observations made on other faunal elements (e.g. brachiopods; Harper *et al.* this volume) and sedimentological data indicating episodic storm deposits smothering autochthonous communities in an otherwise quiet and relatively distal environment (see Saleh *et al.* 2024a; Vaucher *et al.* this volume).

Although diverse (at least six taxa; see above), with around 20 specimens collected over the past six years, echinoderms are a significant but minor component of the Cabrières Biota (Saleh *et al.* 2024a). At Mourèze, the abundance of eocrinoid plates (*Lingulocystis*) in the underlying Foulon Formation suggests that these stemmed blastozoans were probably the dominant group in higher-energy, more proximal settings, where they may have formed eocrinoid meadows. This observation is in good agreement with the sedimentological interpretations proposed for these levels, deposited in shallower and higher energy settings (Courtessole *et al.* 1985, 1991; Dabard & Chauvel 1991; Noffke & Nitsch 1994; Vaucher *et al.* this volume). Therefore, the paucity of echinoderms in the Cabrières Biota cannot be explained simply by the polar, high-latitude position of the southern Montagne Noire during the Early Ordovician (Saleh *et al.* 2024a), but more likely reflects subtle variations in the environment and/or benthic communities.

Furthermore, while the number of echinoderm specimens collected in the Cabrières Lagerstätte may appear relatively low, it should be put into perspective with the corresponding sampling effort elsewhere in the southern Montagne Noire (Table 1). The Early Ordovician echinoderm faunas from the Minervois, Pardailhan, and Mont Peyroux units represent, together with those recently described from the Fezouata Shale (Anti-Atlas, Morocco) and the Ninemile and Fillmore formations (Nevada and Utah, USA), some of the best-studied and most diverse echinoderm assemblages known worldwide for this time interval (Guensburg & Sprinkle 1992; Sprinkle & Guensburg 1997, 2004; Vizcaïno & Lefebvre 1999; Lefebvre *et al.* 2013, 2016). Fully articulated

Table 1. Evolution over time of the number of echinoderm specimens collected in different stratigraphical units of the Lower Ordovician of the Montagne Noire (Minervois, Pardailhan, and Mont Peyroux units) between 1875 and 2024. Numbers refer exclusively to material deposited in the public palaeontological collections of Géosciences Rennes, the Musée du Biterrois (Béziers), the Muséum d'Histoire Naturelle de Toulouse, the Muséum National d'Histoire Naturelle (Paris), the Université Claude Bernard Lyon 1 (Villeurbanne), and the Université de Montpellier.

	1875–1974	**1975–2024**	**TOTAL (specimens)**
upper Landeyran	1	41	42
lower Landeyran	3	154	157
Foulon	4	3	7
Cluse de l'Orb	1	36	37
La Maurerie	12	71	83
upper Saint-Chinian	25	203	228
middle Saint-Chinian	284	158	442
TOTAL (specimens)	330	666	996

echinoderm remains are, however, also extremely rare in the Lower Ordovician deposits of the Minervois, Pardailhan, and Mont Peyroux units (Vizcaïno & Lefebvre 1999). Their knowledge is the result of more than 150 years of active and intensive sampling in the Montagne Noire, which has fueled the regular description of new taxa (e.g. Thoral 1935; Spencer 1951; Fell 1963a, 1963b; Ubaghs 1960, 1961, 1969, 1970, 1972, 1983, 1991, 1994; Daley 1992; Ruta 1997; Lefebvre & Vizcaïno 1999; Dean Shackleton 2005; Nardin 2007; Ewin *et al.* 2020; Dupichaud *et al.* 2023).

The detailed review of Early Ordovician echinoderm remains from the Minervois, Pardailhan, and Mont Peyroux units deposited in major public collections has yielded 996 records of specimens belonging to eight classes and more than 40 taxa (database available at: https://osf.io/g8yhw/). However, about one-third of these specimens were collected in over a century (from the mid-1870s to the mid-1970s) of active sampling, focusing mainly on the fossiliferous concretions of the Saint-Chinian Formation (e.g. Azaïs, Courtessole-Griffe, Escande, Griffe, Guiraud, Lignières, Marty, Miquel, Villebrun, Thoral collections) (Table 1), implying an average of 3.3 specimens collected each year. Over the past 50 years, intensive sampling of echinoderms in all Lower Ordovician formations of the southern Montagne Noire has resulted in the discovery of over 600 additional specimens (e.g. Courtessole-Vizcaïno, Lacombe, Lefebvre, Monceret-Goujon, Reboul, Vizcaïno collections) (Table 1), representing an average of 13.3 specimens collected annually. However, despite a significant sampling effort in the Landeyran Formation over the last 50 years, approximately 150 specimens have been found in this level (Ubaghs 1983, 1991, 1994; Lefebvre & Vizcaïno 1999), representing an average number of approximately three specimens discovered annually (Table 1). These particularly low figures are comparable with those obtained for the Cabrières Lagerstätte (around 20 specimens in six years).

The scarcity of echinoderm remains in the Cabrières Biota therefore represents the rule, rather than the exception, in the Lower Ordovician of the Montagne Noire. However, it is very likely that, similarly to the situation in the Minervois, Pardailhan and Mont Peyroux units, active sampling in the Pic de Vissou unit will contribute to increasing the number of specimens and taxa over the years. In the Lower Ordovician of the Montagne Noire, the scarcity of echinoderms in most levels is comparable to the situation described in several localities in the Fezouata Shale in the central Anti-Atlas of Morocco (Lefebvre *et al.* 2016), which were associated with relatively similar environmental conditions (i.e. an open shelf at/below storm wave base; see Vaucher *et al.* 2016, 2017). In this region, although taxonomically diverse, echinoderms represent minor components of most Floian communities (e.g. at Bou Chrebeb, Bou Zeroual, Toumiat), which are dominated by rhynchonelliform brachiopods, conulariids, hyolithids, molluscs, and trilobites (see e.g. Destombes *et al.* 1985; Vidal 1996b, 1998; Kröger & Lefebvre 2012; Ebbestad 2016; Lefebvre *et al.* 2016; Martin *et al.* 2016; Polechová 2016; Candela *et al.* 2024). In the Zagora area, the same situation has also been documented in the late Tremadocian assemblage of Oued Beni Zoli (Kröger & Lefebvre 2012; Ebbestad & Lefebvre 2015; Lefebvre *et al.* 2016; Kouraïss *et al.* 2019). In the Fezouata Shale, echinoderms are minor components of diverse benthic communities living in nutrient-rich, well-oxygenated, and stable environments (Lefebvre *et al.* 2016). In contrast, they are the dominant group in low-diversity assemblages thriving in more unstable, high-energy and/or dysoxic settings (Lefebvre *et al.* 2016).

The same situation was apparently present in the southern Montagne Noire. In the Mont Peyroux and Pic de Vissou units, the proximal, high-energy sandstones of the Cluse de l'Orb and Foulon formations yielded very low-diversity benthic communities dominated by the eocrinoid *Lingulocystis* associated with inarticulate brachiopods (Vizcaïno & Lefebvre 1999; Vizcaïno *et al.* 2001; Nardin 2007). Similar proximal assemblages dominated by the eocrinoid *Rhopalocystis* are known from the Fezouata Shale in Morocco (Lefebvre *et al.* 2016; Allaire *et al.* 2017). In the uppermost part of the Saint-Chinian Formation (la Grunasse locality), thin, storm-generated sandstone lenses have yielded abundant specimens of a low diversity assemblage dominated by isolated valves (adorals) of kirkocystid mitrates (*Anatifopsis* spp.), associated with relatively common cornute thecal plates and rare other faunal elements (e.g. *Plumulites* shell plates, trilobite fragments) (Lefebvre 2007). A comparable, storm-generated, kirkocystid-dominated assemblage has also been reported from the Lower Ordovician Dumugol Formation of Korea (Lee *et al.* 2005, 2006).

Palaeoenvironmental controls on the distribution of benthic assemblages in the Lower Ordovician of the Montagne Noire

The influence of palaeoenvironmental conditions (e.g. bathymetry, nature of the substrate, oxygenation) on the distribution of Ordovician benthic assemblages has been extensively studied in many regions, leading to the identification of numerous 'communities' or 'biofacies', generally based on taxa, mainly brachiopods and trilobites, adapted to very specific niches (see e.g. Fortey 1975; Fortey & Owens 1978, 1987; Henry 1980; Havlíček 1982; Waisfeld 1995; Vidal 1996b; Zhan *et al*. 2002; Zhiyi *et al*. 2003; Mergl *et al*. 2008; Candela & Hansen 2010; Balseiro *et al*. 2011; Zhou *et al*. 2011; Martin *et al*. 2016; Saleh *et al*. 2018; Serra *et al*. 2021). In comparison, very few studies have been devoted to the palaeoenvironmental distribution of Ordovician echinoderms (see e.g. Bockelie 1984; Sprinkle & Guensburg 1995; Mergl & Prokop 2006; Lefebvre 2007; Botting *et al*. 2013; Lefebvre *et al*. 2016). In the Lower Ordovician of the southern Montagne Noire, the role of environmental conditions on the distribution of benthic faunas has been little studied so far, with only a few studies focusing on trilobites (Courtessole *et al*. 1991; Henry & Vizcaïno 1996; Vidal 1996a; Vizcaïno *et al*. 2001; Vizcaïno & Álvaro 2003) and echinoderms (Vizcaïno & Lefebvre 1999; Nardin 2007).

Environmental control of trilobite assemblages

Although the southern part of the Montagne Noire has yielded a great diversity of trilobites, this diversity is not homogeneous across the entire succession. The successive geological units provide a continuous sedimentary record from the Tremadocian to the Floian with, in ascending order: the Saint-Chinian, La Maurerie, Cluse de l'Orb, Foulon (including the Setso Member), and Landeyran formations (Fig. 2). Based on previous publications, two peaks of trilobite diversity are particularly remarkable: the first one is located in the middle part of the Saint-Chinian Formation (*Euloma filacovi* Zone), and the second in the lower part of the Landeyran Formation (*Apatokephalus incisus* Zone; Fig. 2), with respectively 26 and 19 genera (Vizcaïno *et al*. 2001; Vizcaïno & Álvaro 2003).

Middle Saint-Chinian trilobite assemblage.– In addition to agnostids, the *Euloma filacovi* Zone has yielded numerous asaphids, as well as Eulominae, Nileidae (*Aocaspis*, *Symphysurus*), Raphiophoridae (*Ampyx*, *Ampyxinella*), and *Prionocheilus*, generally associated with more or less distal shelf environments. In addition to these frequent taxa, some rare but typical forms of distal environments (i.e. talus or even oceanic basin) are present such as the cyclopygids *Degamella* and *Novakella*, as well as *Bohemilla* (Bohemillidae) and *Illaenopsis* (Nileidae) (Courtessole *et al*. 1985; Vizcaïno *et al*. 2001; Vizcaïno & Álvaro 2003). The mixture of taxa is likely related to transgressive pulses. It reflects incursions of deep-sea assemblages into the mid-to-distal shelf environment (lower offshore), characterized by the raphiophorid biofacies (Fortey & Owens 1978, 1987; Vidal 1996b; Martin *et al*. 2016). Among this assemblage (Fig. 6), the absence of olenids, present in the underlying La Dentelle Formation (Vizcaïno *et al*. 2001) and generally described in distal dysoxic to anoxic deposits of the Lower Ordovician (Fortey & Owens 1978; Fortey 2000), is notable.

Upper Saint-Chinian, La Maurerie and Setso deposits trilobite assemblage. – The uppermost part of

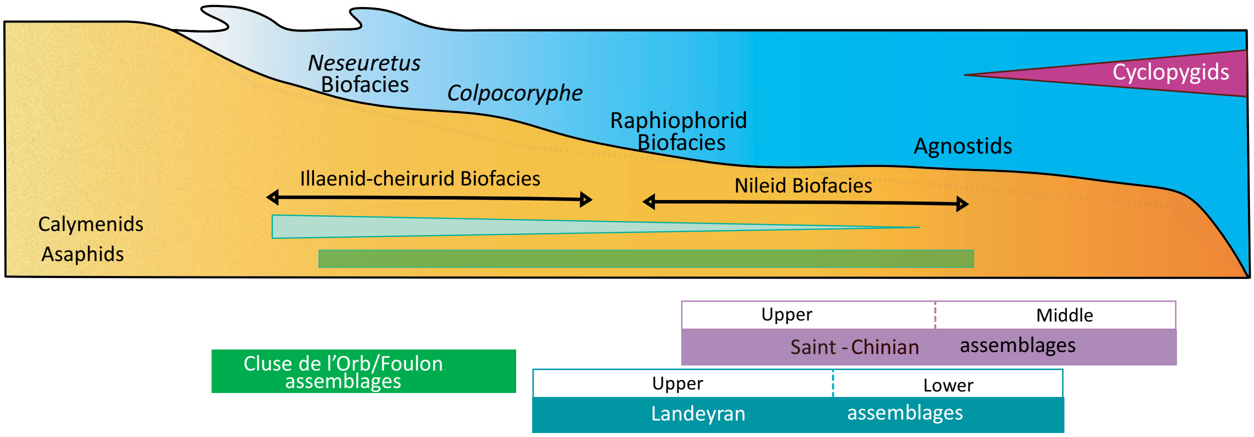


Fig. 6. Depositional environments of the Lower Ordovician of the Montagne Noire based on trilobite assemblages from the Minervois, Pardailhan, and Mont Peyroux units and the distribution model of trilobite assemblages on a proximal-distal depositional profile from the Ordovician of the Gondwanan margin (Fortey & Owens 1978, 1987; Vidal 1996b) and the Czech Republic (Mergl 2006; Mergl *et al*. 2008).

the Saint-Chinian Formation and the overlying La Maurerie Formation (*Asaphelina barroisi berardi* + *Taihungshania miqueli* and *T. miqueli* acme subzones; Fig. 2) also yielded abundant asaphids and raphiophorids. However, trilobite diversity is drastically reduced compared to the underlying *E. filacovi* Zone, with the disappearance of all taxa typical of deep-sea environments. This latest Tremadocian – early Floian assemblage corresponds to the raphiophorid biofacies associated with the lower part of the upper offshore and/or the upper part of the lower offshore, without any influence of the oceanic fauna (Fig. 6). This trend towards shallower environments continues in the overlying Setso Member (*Taihungshania shui landayranensis* Zone), which yielded a low-diversity assemblage restricted to asaphids and taihungshaniids, while raphiophorids disappeared (Vizcaïno & Álvaro 2003).

Cluse de l'Orb and Foulon trilobite assemblage.– In the *Colpocoryphe maynardensis* and *Neseuretus (N.) arenosus* zones (Fig. 2), calymenid trilobites become abundant with representatives of the genera *Colpocoryphe*, *Neseuretus* and *Pradoella* co-occuring with Taihungshaniidae and asaphids (Courtessole *et al.* 1983, 1985; Vizcaïno *et al.* 2001; Vizcaïno & Álvaro 2003). Calymenids are typically benthic to endobenthic trilobites (Hammann 1985), associated with soft, well-oxygenated substrates of proximal to median shelf environments (distal shoreface to upper offshore) with the well-known *Neseuretus* biofacies (Fig. 6), which is the most proximal one (Fortey & Owens 1978; Fortey & Morris 1982; Henry 1989; Waisfeld 1995; Vidal 1996b). Some species of *Colpocoryphe*, a genus usually restricted to proximal to median shelf environments (Vidal 1996b), may extend to deeper settings. In this case, trilobites are often characterized by reduced eyes or blindness (Henry *et al.* 1997). In the Montagne Noire succession, calymenids have normal-sized eyes and correspond, in most cases, to disarticulated specimens, highlighting the energetic conditions that remobilized sediment and carapaces before their definitive burial in proximal settings. Consequently, the trilobites suggest a continuous shallowing trend, with more and more proximal successive assemblages, from the Saint-Chinian Formation to the Cluse de l'Orb and Foulon formations (Fig. 6).

Landeyran trilobite assemblage.– The Landeyran Formation is divided into two parts: the lower part corresponds to the *Apatokephalus incisus* Zone, and the upper part to the *Hangchungolithus primitivus* Zone (Fig. 2). The trilobite assemblage of the lower part of the Landeyran Formation is well diversified (19 genera) and is dominated by asaphids and raphiophorids, associated with rare specimens of *Colpocoryphe* and the reappearance of agnostids. Proximal trilobites such as *Neseuretus* and *Pradoella* are replaced by taxa typical of the raphiophorid biofacies (Fig. 6), as well as by *Apatokephalus*, cheirurids (*Foulonia* and *Pliomerops*), some cyclopygids (e.g. *Incisopyge* and *Carolinites*), *Euloma*, and *Selenopeltis* (Vizcaïno *et al.* 2001; Vizcaïno & Álvaro 2003). This assemblage reflects a major faunal and environmental change with the underlying Cluse de l'Orb and Foulon formations (Fig. 6). The oceanic influence appears less marked than in the middle part of the Saint-Chinian Formation. However, the Landeyran trilobite assemblage reflects a clear transgressive trend and the appearance of more distal offshore environmental conditions (Courtessole *et al.* 1991; Henry & Vizcaïno 1996; Vizcaïno *et al.* 2001; Vizcaïno & Álvaro 2003). The upper part of the Landeyran Formation, although presenting quite similar sedimentological facies, yielded *Neseuretus*, *Pradoella* and *Platycoryphe* (Homalonotidae), which are usually associated with *Colpocoryphe* (Calymenidae), *Hangchungolithus* (Trinucleidae), and *Toletanapis* (Zeliskellinae), in addition to widespread asaphids (Vizcaïno *et al.* 2001; Vizcaïno & Álvaro 2003). This trilobite assemblage corresponds to shallower environments with the return of numerous calymenids and *Toletanaspis*, whereas these taxa are rare in the lower part of the Landeyran Formation (Henry *et al.* 1992). The diversity of this assemblage is nevertheless greater than in the *Neseuretus* biofacies, suggesting an environment intermediate between this biofacies and that of the raphiophorid biofacies (Fig. 6).

Summary.– In summary, trilobite assemblages show a significant shallowing trend from the Saint-Chinian Formation (distal shelf environmental conditions: lower offshore) to the Cluse de l'Orb and Foulon levels (delta-front to upper offshore), before returning to median to distal shelf environmental conditions in the lower part of the Landeyran Formation (Fig. 6). The upper part of this latter stratigraphical unit records a further shallowing trend (Fig. 6). Very similar trends have been described for conulariids (Van Iten & Lefebvre 2020) and echinoderms (see below; Vizcaïno & Lefebvre 1999), with comparable, high-diversity, distal assemblages in the Saint-Chinian and Landeyran formations, and more proximal, low-diversity communities in the Cluse de l'Orb and Foulon formations (Nardin 2007).

Environmental control on echinoderm assemblages

The elaboration of a comprehensive dataset compiling all Early Ordovician echinoderm specimens from the Minervois, Pardailhan and Mont Peyroux units deposited in the main public collections offers the opportunity to identify unique echinoderm assemblages (Figs 2, 7), and to explore environmental conditions involved into the temporal evolution of taxonomically and ecologically coherent echinoderm communities.

Middle Saint-Chinian echinoderm assemblage.– The *Euloma filacovi* Zone has yielded the most abundant and taxonomically diverse echinoderm assemblage, with 28 described taxa belonging to nine classes (Figs 7, 8). However, most specimens (86%) belong to only nine taxa. The middle Saint-Chinian assemblage is dominated by the cornutes *Phyllocystis blayaci* and *P. crassimarginata*, associated with the somasteroid *Chinianaster levyi*, the stenuroid *Pradesura jacobi*, the crinoid *Aethocrinus moorei*, the glyptocystitid rhombiferan *Macrocystella azaisi*, the two peltocystid mitrates *Anatifopsis trapeziiformis* and *Peltocystis cornuta*, and the solutan *Minervaecystis vidali*. The other 19 echinoderm taxa identified in the middle Saint-Chinian assemblage are each known by a handful of specimens (often only one or two), and can therefore be considered as rare taxa. The echinoderms of the middle Saint-Chinian assemblage therefore form a relatively diverse community, dominated by representatives of six different classes (Crinoidea, Rhombifera, Soluta, Somasteroidea, Stenuroidea, and Stylophora), but constituting only a minor component of the overall benthic community, dominated by brachiopods, molluscs, and trilobites (see Thoral 1935; Courtessole *et al.* 1981, 1983; Babin *et al.* 1982; Vizcaïno *et al.* 2001).

This assemblage from the southern Montagne Noire shares several taxa, even at species level (e.g. the solutan *Plasiacystis mobilis*, and the stylophorans *Amygdalotheca griffei*, *Anatifopsis trapeziiformis*, *Chauvelicystis vizcainoi*, *Peltocystis cornuta*, *Phyllocystis blayaci*, and *Vizcainocarpus dentiger*) with echinoderm communities present in the lower part of the Fezouata Shale (Morocco), which have the same age (late Tremadocian) and are also associated with soft siliciclastic substrates, at or below the storm wave

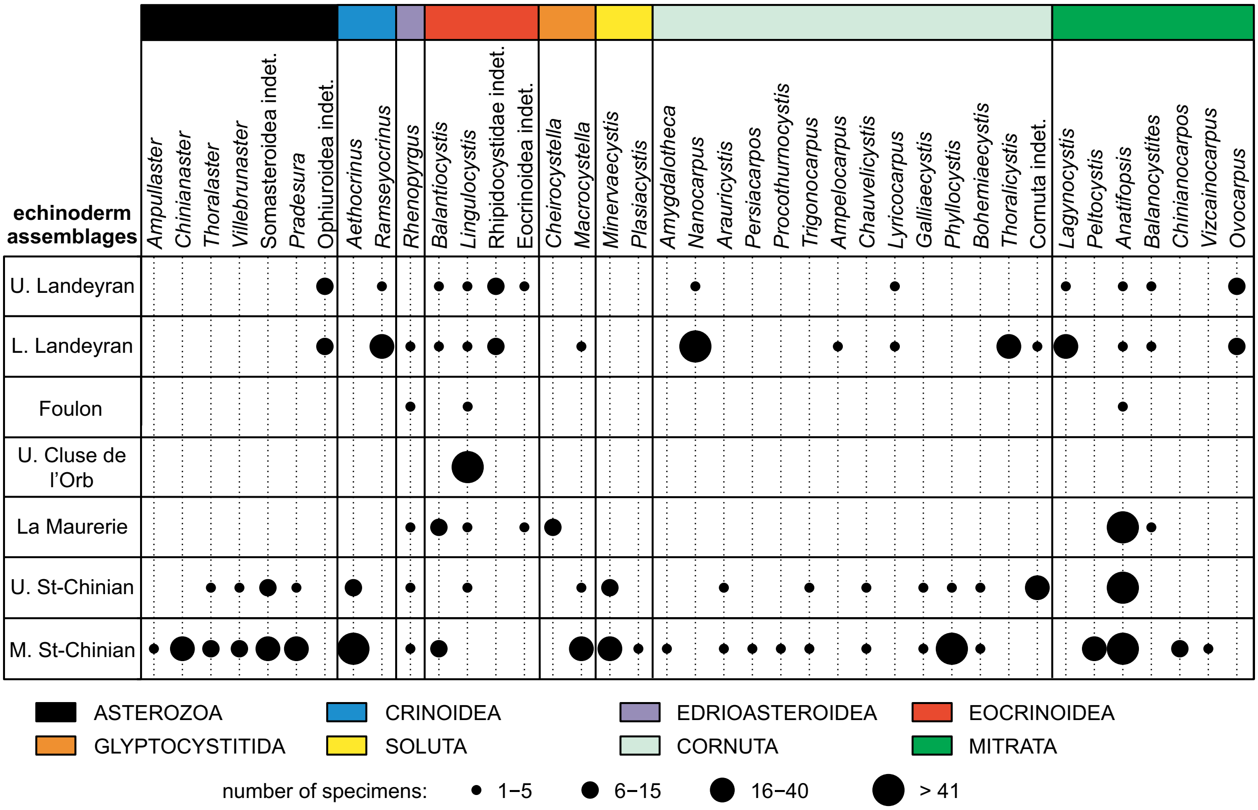


Fig. 7. Variation in the abundance of Early Ordovician echinoderms from the southern Montagne Noire, based on specimens from the Minervois, Pardailhan, and Mont Peyroux units deposited in public collections.

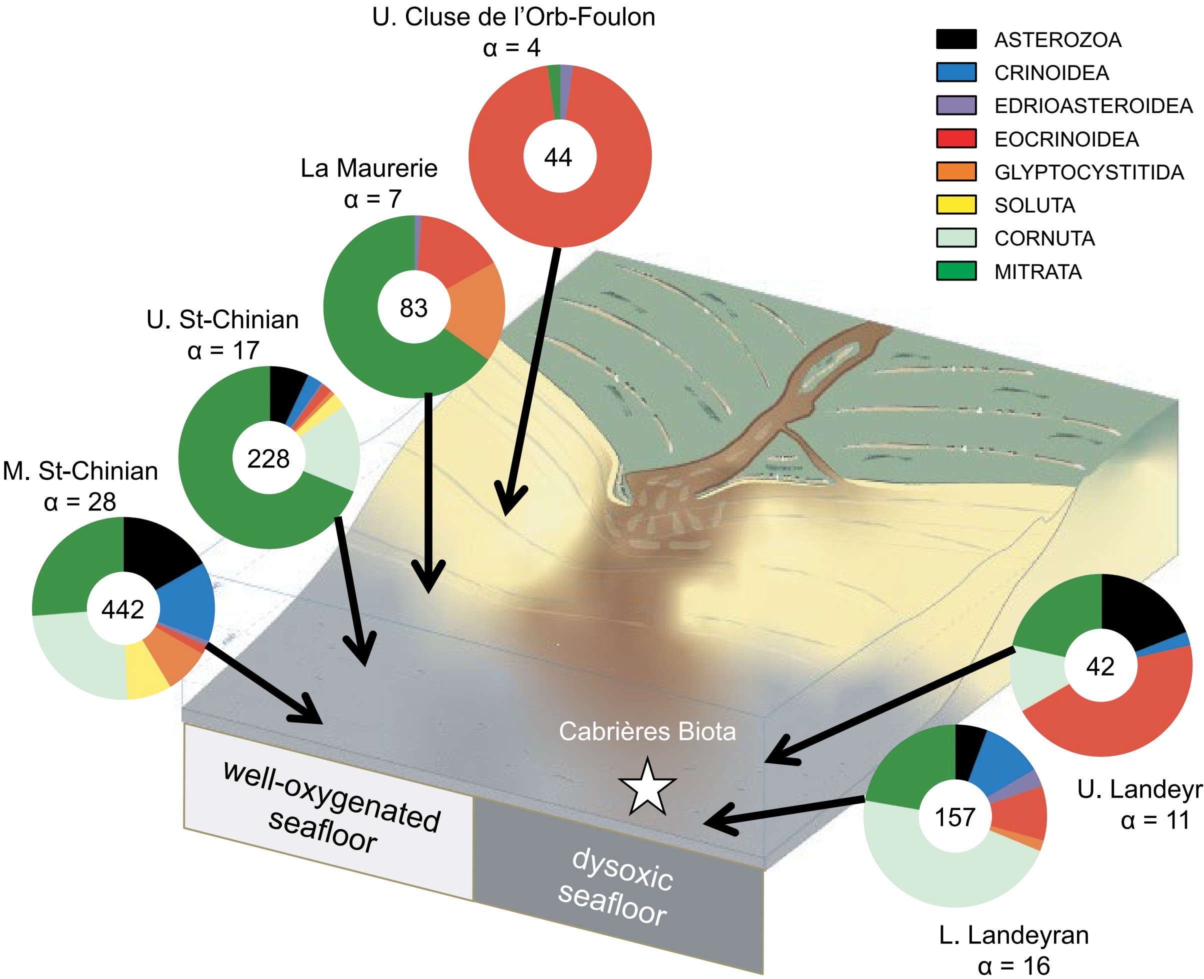


Fig. 8. Spatial distribution and taxonomic composition of the six main successive echinoderm assemblages from the Lower Ordovician of the Montagne Noire. For each assemblage, the number of analysed specimens is indicated within the pie chart, while the total number of identified taxa (α diversity) is indicated next to it. The presumed palaeoenvironmental context of the Cabrières Biota is indicated by a white star. Conceptual model of deposition modified from Vaucher *et al.* (this volume).

base (Lefebvre *et al.* 2016). However, unlike the situation in the Montagne Noire, most Moroccan assemblages are each dominated by one or two echinoderm taxa (mainly cornutes and/or eocrinoids) and are associated with a very low-diversity fauna (e.g. inarticulate brachiopods, graptolites) (Martin *et al.* 2015; Lefebvre *et al.* 2016, 2019). Another difference concerns the size of the individuals: representatives of the same taxon are generally half as small in the lower part of the Fezouata Shale as in the Saint-Chinian Formation (Lefebvre *et al.* 2016). In these levels of the Fezouata Shale, the small size of echinoderms cannot be explained by oligotrophic conditions, because abundant acritarch remains are found in the associated deposits (Nowak *et al.* 2016). The small size of the echinoderms and the low-diversity of their associated fauna probably result from the existence of relatively unstable, often dysoxic environmental conditions, which were probably favorable to the establishment of extensive, short-lived and opportunistic echinoderm dense beds, but prevented the colonisation of the seafloor by more diverse and structured 'middle Saint-Chinian-like' communities dominated by molluscs and trilobites (Lefebvre *et al.* 2016).

In contrast, several examples of taxonomically diverse echinoderm communities comparable to the middle Saint-Chinian assemblage (i.e. including asterozoans, crinoids, eocrinoids, glyptocystitids, solutans, and stylophorans) are known from several Early Ordovician localities worldwide. They generally represent minor components of particularly diverse benthic communities inhabiting relatively distal, well-oxygenated, soft sea-bottoms (Fig. 8). Examples of such communities have been described from some upper Tremadocian (e.g. Oued Beni Zoli) and most lower to middle Floian localities in the Anti-Atlas, Morocco (Lefebvre *et al.* 2016; Kouraïss *et al.* 2019), as well as in the Lower Ordovician Fillmore Formation (Utah) and the Ninemile Shale (Nevada) (Guensburg & Sprinkle 1992, 2001, 2003; Sprinkle & Guensburg 1995; Blake & Guensburg 2005; Blake *et al.* 2007; Sumrall *et al.* 2012).

Upper Saint-Chinian echinoderm assemblage.– The uppermost part of the Saint-Chinian Formation (*A. barroisi berardi* + *T. miqueli* Subzone; Fig. 2) yielded a lower diversity echinoderm community (17 taxa), which represents an impoverished subset of the underlying assemblage (Figs 7, 8). However, except for crinoids (*Aethocrinus*), solutans (*Plasiacystis*) and somasteroids, which remain relatively common, most other echinoderms (including the cornute *Phyllocystis*) are represented by very few individuals and can be considered rare taxa. As in the underlying *E. filacovi* Zone, echinoderms represent a minor component of an otherwise diverse benthic community, dominated by rhynchonelliform brachiopods, molluscs, and trilobites (e.g. Thoral 1935; Vizcaïno *et al.* 2001). The upper Saint-Chinian echinoderm assemblage is also characterized by the appearance of the eocrinoid *Lingulocystis elongata*, which is generally associated with more proximal environmental conditions (Vizcaïno & Lefebvre 1999; Nardin 2007). However, most specimens of the upper Saint-Chinian echinoderm assemblage (~80%) were collected from storm-generated lenticular sandstone deposits, which yielded low-diversity faunas dominated by kirkocystid mitrates (*Anatifopsis* spp.) associated with disarticulated cornute remains, and rare fragments of other organisms (machaeridians, trilobites) (see above; Lefebvre 2007). These levels are typical of the Ordovician 'kirkocystid biofacies' *sensu* Lefebvre (2007), which is associated with well-oxygenated soft substrates, at or above storm-wave base, under locally and/or temporally unstable, high-energy environmental conditions, unfavorable for the establishment of more diverse communities. Although it shares several taxa with the middle Saint-Chinian assemblage, the upper Saint-Chinian assemblage therefore represents a taxonomically less diverse community, characterized by the absence of mitrocystitid mitrates, the scarcity of cornutes and *Macrocystella*, and the local abundance of kirkocystids, which together with the presence of rare individuals of *L. elongata* suggests subtle environmental changes and slightly more proximal conditions, with more frequent and thicker storm-generated deposits.

La Maurerie echinoderm assemblage.– In the overlying La Maurerie Formation (*Taihungshania miqueli* acme Zone; Fig. 2), echinoderms represent a very minor component of particularly diverse benthic communities dominated by rhynchonelliform brachiopods, molluscs and trilobites. In these layers, echinoderm remains are not only rare but also poorly diversified (7 taxa; Figs 7, 8). Their scarcity does not result from a sampling bias, as abundant and well-preserved invertebrate faunas have been collected from these layers over a long period of time (e.g. Thoral 1935; Babin *et al.* 1982; Courtessole *et al.* 1983; Vidal 1996a; Vizcaïno *et al.* 2001). The La Maurerie echinoderm assemblage is dominated by kirkocystid mitrates (*Anatifopsis* spp.), associated with relatively common eocrinoids (mainly *Balantiocystis thorali*, with rare specimens of *Lingulocystis elongata*) and the glyptocystitid rhombiferan *Cheirocystella languedociana*. Asterozoans, cornutes, crinoids, mitrocystitid mitrates, and solutans appear to be absent from these levels. The absence of these taxa, as well as the occurrence of abundant kirkocystids, the presence of *Lingulocystis elongata*, and the replacement of *Macrocystella* by *Cheirocystella* indicate that the low-diversity La Maurerie echinoderm assemblage was associated with well-oxygenated soft substrates, in higher energy and more proximal environments than those present in the underlying Saint-Chinian Formation (Vizcaïno & Lefebvre 1999).

Echinoderm remains are totally absent in the lower part of the Cluse de l'Orb Formation (Fig. 2). The sedimentological interpretation of these levels suggests that they were deposited in a prodelta, with hyperpycnal flows developing during flood discharges (Vaucher *et al.* this volume). These river-dominated environmental conditions, with strong variations in salinity, were therefore inhospitable for stenohaline, fully marine organisms, such as echinoderms.

Upper Cluse de l'Orb-Foulon echinoderm assemblage.– In the upper part of the Cluse de l'Orb Formation and the overlying Foulon Formation (Fig. 2), sedimentary structures and associated trace fossils (e.g. *Daedalus*) document the transition towards wave-dominated, high-energy, shoreface to upper offshore settings (Gougeon *et al.* this volume; Vaucher *et al.* this volume). In these proximal environments, echinoderms are a major component of low-diversity benthic marine communities inhabiting soft siliciclastic substrates. The upper Cluse de l'Orb-Foulon echinoderm assemblage consists almost exclusively of abundant and usually disarticulated skeletal remains of *Lingulocystis* (Figs 7, 8). Fully articulated specimens are rare, but can sometimes be preserved in thick storm deposits. While *Lingulocystis elongata* is the dominant form in the upper part of the Cluse de l'Orb Formation, it appears to have been replaced by *L.* aff. *deani* in the overlying Foulon Formation (Nardin 2007). In these levels, the massive presence of skeletal remains of *Lingulocystis* spp. suggests that these eocrinoids formed extensive meadows over the sea floor (Vizcaïno & Lefebvre 1999; Nardin 2007). Comparable nearshore, eocrinoid-dominated communities were reported in the Lower Ordovician Fezouata Shale in the Central Anti-Atlas, Morocco (Allaire *et al.* 2015, 2017; Lefebvre *et al.* 2016), the Middle Ordovician Moitiers d'Allonne Formation in Normandy, France (Régnault 1990), and the Upper Ordovician Izegguirène Formation in the Tafilalt, Morocco (Nardin & Régnault 2015; Lefebvre *et al.* 2022b).

Lower Landeyran echinoderm assemblage (Cabrières Biota).– In levels corresponding to the overlying *Apatokephalus incisus* Zone, the dark siltstones of the lower part of the Landeyran Formation have yielded abundant remains of a diverse echinoderm assemblage (16 taxa belonging to six classes; Fig. 2). The lower Landeyran echinoderm assemblage is dominated by the cornute *Nanocarpus dolambii*, associated with relatively common taxa including the two scotiaecystid cornutes *Thoralicystis melchiori* and *T.*? *ubaghsi*, the crinoid *Ramseyocrinus vizcainoi*, the mitrates *Lagynocystis pyramidalis* and *Ovocarpus moncereti*, the glyptocystitid *Macrocystella* sp., as well as yet undescribed ophiuroids and rhipidocystid eocrinoids (Figs 7–9). Most other taxa are known from a limited number of specimens. The relatively diverse echinoderm remains collected from the Pic de Vissou unit (Cabrières Biota; Fig. 5), which comprise *Balantiocystis* sp., *Macrocystella* sp., *N. dolambii*, *Ovocarpus moncereti*, rhipidocystid eocrinoids, and *T.*? *ubaghsi*, therefore represent a typical subset of the lower Landeyran assemblage (Fig. 9).

In many respects, the composition of the lower Landeyran assemblage shares several similarities with that of the middle Saint-Chinian assemblage (Fig. 7; Vizcaïno & Lefebvre 1999). In both cases, cornutes contribute significantly to an otherwise relatively diverse echinoderm community composed of abundant asterozoans, crinoids, eocrinoids (*Balantiocystis*), glyptocystitids (*Macrocystella*), and mitrates. These two echinoderm assemblages also represent minor components of particularly diverse benthic communities dominated by brachiopods, molluscs, and trilobites (see e.g. Dean 1966; Babin *et al.* 1982; Courtessole *et al.* 1983, 1991; Vizcaïno *et al.* 2001). It is therefore very likely that both echinoderm assemblages inhabited soft substrates in relatively comparable, distal and quiet (below storm-wave base) settings (Vizcaïno & Lefebvre 1999; Vizcaïno *et al.* 2001). However, the middle Saint-Chinian and lower Landeyran echinoderm assemblages also show significant differences, which may reflect original differences in the associated environmental conditions.

A first striking difference concerns the size of the specimens. With the possible exception of *Ramseyocrinus* (Fig. 9B), most taxa in the *A. incisus* Zone are characterized by a very small size. For example, the theca of most stylophorans (*Ampelocarpus landeyranensis*, *Nanocarpus dolambii*, *Ovocarpus moncereti*, *Thoralicystis*? *ubaghsi*) is only 3–10 mm long. The mitrate *Lagynocystis pyramidalis* (Fig. 9D) can reach larger sizes (10–15 mm), comparable to those observed in the lower part of the Fezouata Shale in Morocco (Lefebvre *et al.* 2016), but about half as small as in the Middle Ordovician of the Prague Basin and southeastern Brittany (Barrande 1887; Henry *et al.* 1997; Lefebvre 2007). Although *Balantiocystis* and *Macrocystella* both occur in the two assemblages, specimens from the *E. filacovi* Zone are consistently 1.5 to 2 times larger than those from the *A. incisus* Zone. In fact, this size reduction affects not only echinoderms, but also other members of the associated benthic community (e.g. brachiopods; see Harper *et al.* this volume).

Size reduction in marine invertebrates is often linked to stressful environmental conditions, such as physical disturbance caused by storms, high predation pressure, oligotrophy, and/or oxygenation (see Tasch 1953; Twitchett 2007; He *et al.* 2010, 2017; Saleh *et al.* 2018, 2021b). Physical disturbance caused by storms or turbidity currents was limited: the detailed sedimentological analysis of the lower part of the Landeyran Formation (Vaucher *et al.* this volume) shows evidence of weak turbidity currents reaching the basin floor in the deepest-water facies (in F1 and F2). These very thin beds, together with associated trace fossils (Gougeon *et al.* this volume), demonstrate that these deposits record quiet, distal, open shelf settings, below storm-wave base. Cephalopods, the main predators of Early Ordovician ecosystems (Kröger *et al.* 2009), are relatively diverse and abundant in the Saint-Chinian and Landeyran formations (Thoral 1935; Kröger & Evans 2011; Polechová *et al.* this volume). It is therefore unlikely that the observed size reduction results from an increase in predation pressure. Similarly, a possible oligotrophy can be ruled out given the presence of palynomorphs (acritarchs)

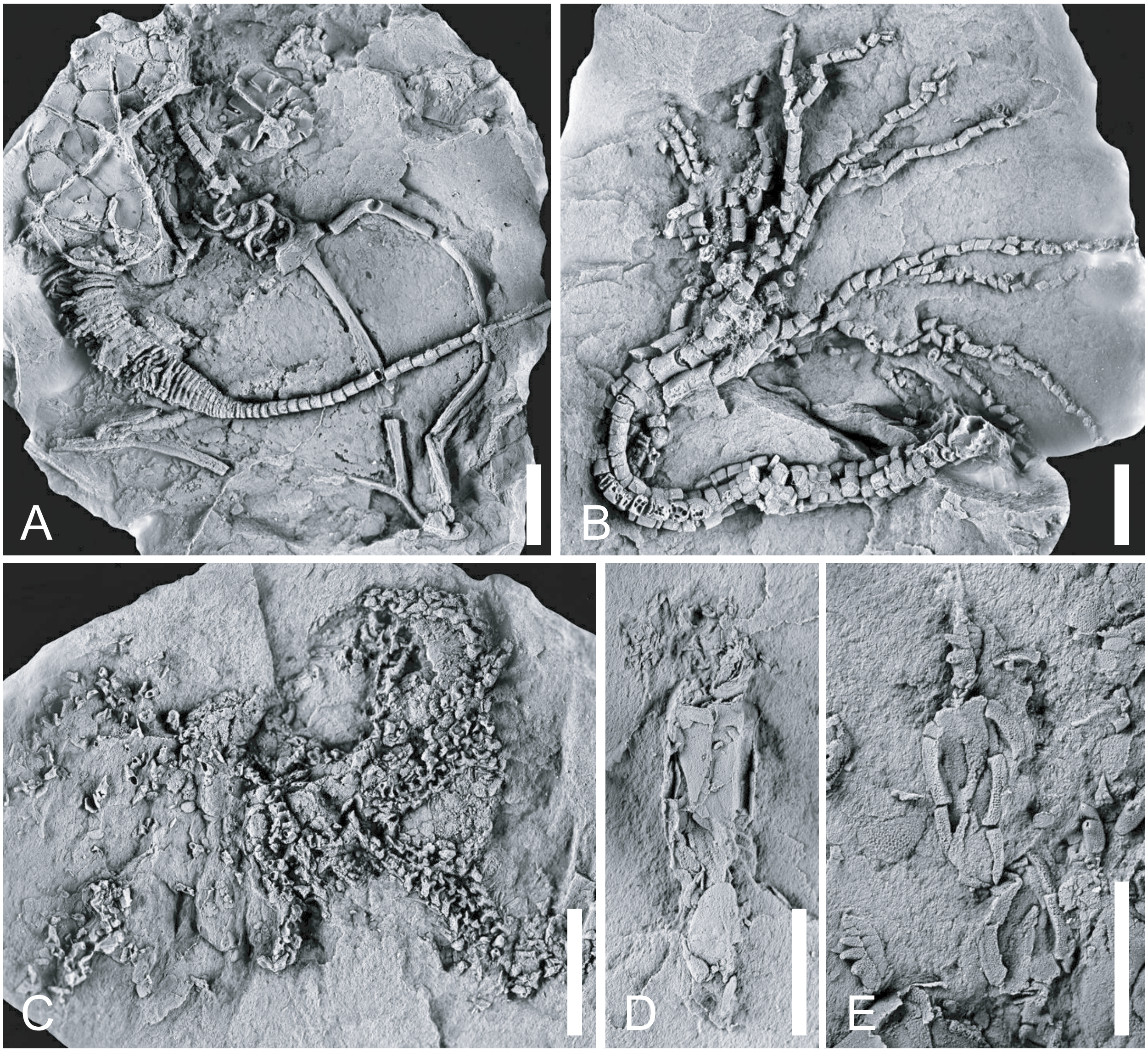


Fig. 9. Echinoderms from the lower part of the Landeyran Formation (*A. incisus Zone*, late Floian), Mont Peyroux unit, southern Montagne Noire. A, association of a fully articulated glyptocystitid (*Macrocystella* sp.) with a slightly disarticulated cornute (*Thoralicystis melchiori*) in lower aspect, UCBL-FSL 712 564. B, *Ramseyocrinus vizcainoi* (Crinoidea): almost complete, slightly disarticulated specimen, with arms, calyx, and stem in connection; UCBL-FSL 712 814 (holotype). C, partly disarticulated ophiuroid indet., UCBL-FSL 424 939. D, *Lagynocystis pyramidalis* (Mitrata): slightly disarticulated theca and proximal aulacophore, in lower aspect, UCBL-FSL 713 158. E, *Nanocarpus dolambii* (Cornuta): cluster of several individuals showing different stages of disarticulation, UCBL-FSL 712 522. All scale bars: 5 mm.

that are particularly abundant in the deposits of the Landeyran Formation (see above; Caillaud *et al*. this volume).

In the lower part of the Landeyran Formation, the existence of dysoxic conditions within the sea floor (and at the sea-substrate interface?) therefore represents the most likely explanation for the observed size reduction in echinoderms and other benthic organisms. This interpretation is supported by trace fossils, consisting for instance of simple horizontal trails (e.g. *Helminthoidichnites tenuis*, *Helminthopsis granulata*) demonstrating semi-infaunal microbial grazing, while vertical burrows (e.g. *Skolithos linearis*) are extremely rare and only found in storm deposits of the lowermost part of the formation (Gougeon *et al.* this volume; Vaucher *et al.* this volume). In levels corresponding to the *A. incisus* Zone, the massive appearance of the mitrate *Lagynocystis pyramidalis* (Fig. 9D), which is the second most abundant taxon (11.5% of the specimens), represents further evidence supporting the existence of dysoxic conditions on the sea floor. In the Lower Ordovician of Morocco (Lefebvre *et al.* 2016), the Middle Ordovician of the Czech Republic, France, and Wales (Barrande 1887; Chauvel & Nion 1977; Jefferies 1987) and the Upper Ordovician of France (Lefebvre *et al.* 2010), the massive appearance of this mitrate is systematically associated with the presence of deep, dysoxic settings (Henry *et al.* 1997; Lefebvre 2007).

A second difference between the middle Saint-Chinian and lower Landeyran echinoderm assemblages concerns their taxonomic diversity and composition (Figs 7, 8). The lower diversity in the *A. incisus* Zone, however, could result, at least in part, from a less intensive sampling effort (see above). Echinoderms from the Saint-Chinian Formation have been collected as early as the 1870s (e.g. Lignières collection), their presence was mentioned in the 1910s (Miquel 1912; Bather 1913), and the first taxonomic descriptions were made by Thoral (1935). In contrast, the occurrence of echinoderm remains in the Landeyran Formation was initially reported only by Dean (1966), while their first descriptions were made by Ubaghs (1983, 1991, 1994). It is therefore probable that several rare taxa have not been collected yet in the Landeyran Formation. With this limitation in mind, some significant differences between the two assemblages concern the possible total absence of solutans and somasteroids, as well as the rarity of kirkocystid mitrates (*Anatifopsis* spp., *Balanocystites* aff. *primus*) in the lower Landeyran assemblage, whereas these groups are major faunal elements of the middle Saint-Chinian assemblage. Solutans were active epibenthic detritus feeders (see e.g. Kolata *et al.* 1977; Jefferies 1990; Noailles *et al.* 2014; Nohejlová & Lefebvre 2022; Dupichaud *et al.* 2023). In the *A. incisus* Zone, their absence could be related to the existence of dysoxic substrates. In the lower part of the Landeyran Formation, the absence of somasteroids, while ophiuroids are relatively common, is also intriguing and calls into question the existence of different feeding strategies in the two groups of asterozoans (detritus-feeding and predation, respectively). Kirkocystids are abundant in a wide range of well-oxygenated offshore settings (see above; Lefebvre 2007). Their scarcity in the lower part of the Landeyran Formation is therefore probably related to the existence of dysoxic conditions.

Upper Landeyran echinoderm assemblage.– The upper part of the Landeyran Formation (*Hangchungolithus primitivus* Zone; Fig. 2) has yielded a relatively similar assemblage, forming a rare, but relatively diverse (11 taxa belonging to four classes; Figs 7, 8) component of small-sized benthic communities dominated by brachiopods, molluscs and trilobites (see e.g. Dean 1966; Babin *et al.* 1982; Courtessole *et al.* 1983, 1991; Vizcaïno *et al.* 2001; Vizcaïno & Álvaro 2003). The upper Landeyran echinoderm assemblage is dominated by a yet undescribed rhipidocystid, associated with relatively common ophiuroids and the mitrate *Ovocarpus moncereti* (Figs 7, 8). The presence of *Lagynocystis pyramidalis*, the rarity of kirkocystids, and the absence of both solutans and somasteroids suggest the persistence of relatively dysoxic environmental conditions. The main differences with the underlying lower Landeyran echinoderm assemblage consist in the scarcity of cornutes (including *Nanocarpus dolambii*, which was the dominant taxon in the *A. incisus* Zone), crinoids (*Ramseyocrinus vizcainoi*) and lagynocystid mitrates, as well as in the rarity (and possibly total absence) of *Macrocystella*.

In many respects, the transition between the lower and the upper Landeyran echinoderm assemblages is reminiscent of the transition between the middle and the upper Saint-Chinian assemblages. In both cases, taxonomic diversity decreases (both at class, genus, and species levels), cornutes no longer constitute the dominant group, and many taxa, which contributed substantially to the diversity of the assemblage (e.g. crinoids, *Macrocystella*) become rare and/or are totally absent. These similar trends suggest a probable comparable transition towards slightly more proximal shelf environments, at or below storm wave base (Fig. 8). However, while the middle and upper Saint-Chinian assemblages inhabited well-oxygenated soft sea bottoms (abundance of kirkocystids, presence of solutans and somasteroids), the lower and upper Landeyran assemblages are associated with dysoxic substrates (presence of *Lagynocystis*, rarity of kirkocystids, absence of solutans and somasteroids) (Fig. 8).

Multivariate analyses of echinoderm assemblages.– Multivariate analyses robustly partition echinoderm assemblages into four statistically distinct faunal communities driven by environmental conditions (Fig. 10). These communities represent recurring taxonomic associations characterized by consistent patterns of species dominance and relative abundance (see Figs 6, 10A, and supplementary data for detailed explanations). The upper Cluse de l'Orb - Foulon assemblage is characterized by its very low richness and abundance, overwhelmingly dominated by *Lingulocystis* spp., representative of nearshore, high-energy, well-oxygenated shoreface environments (Fig. 8). The middle and upper Saint-Chinian assemblages form a coherent community dominated by *Anatifopsis* and associated cornutes, reflecting well-oxygenated

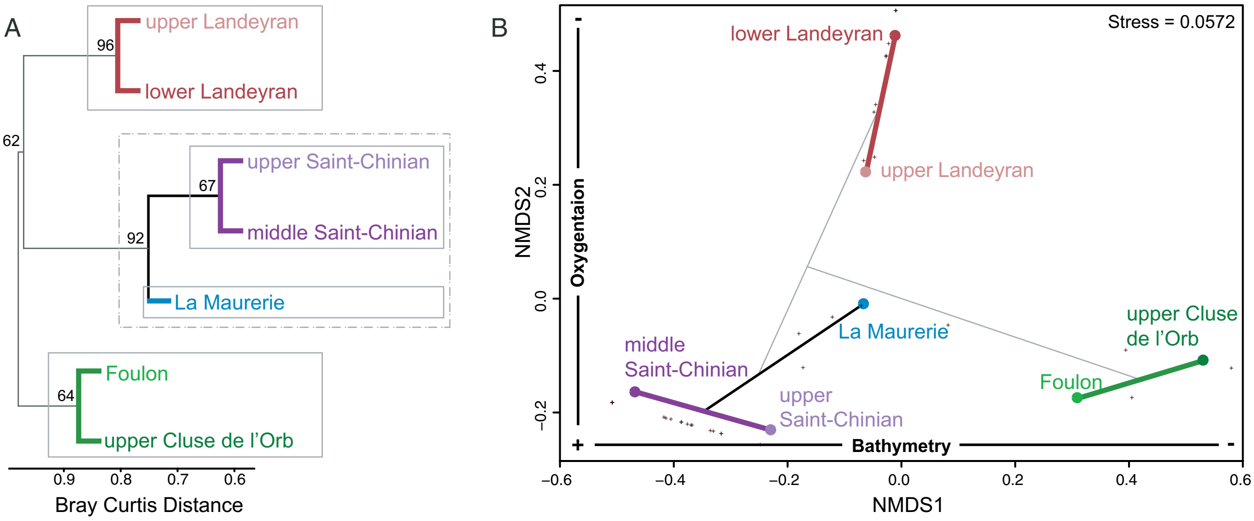


Fig. 10. Multivariate analyses of echinoderm faunal assemblages from the Lower Ordovician of the southern Montagne Noire. A, UPGMA hierarchical clustering based on a Bray-Curtis dissimilarity matrix of species abundances. Numbers at nodes indicate bootstrap support values (1000 replicates). Significant clusters sustained by the simprof and permanova tests are highlighted by different colours and surrounding grey squares. B, non-metric Multidimensional Scaling (NMDS) ordination, with the minimum spanning tree, calculated from the same dissimilarity matrix (2D stress = 0.0572). Each dot represents a locality, coloured according to the clusters identified in (A), with crosses represent species distribution. Post-hoc fitted environmental vectors show the direction of maximum correlation with oxygenation (significant, PERMANOVA $p < 0.01$) and bathymetry (not significant, PERMANOVA $p > 0.05$).

offshore to distal shelf settings with relatively unstable, storm-influenced conditions. In contrast, the La Maurerie assemblage forms a distinct and isolated community despite sharing several taxa, notably *Anatifopsis* spp., with the Saint-Chinian assemblages. This separation reflects a sharp decrease in taxonomic richness and abundance, as well as a turnover in eocrinoid and glyptocystitid rhombiferan taxa, associated with more proximal, higher-energy conditions that limited the establishment of diverse echinoderm communities. Finally, the lower and upper Landeyran assemblages form a statistically robust cluster characterized by the co-dominance of *Nanocarpus*, *Lagynocystis*, *Ovocarpus*, *Ramseyocrinus*, and scotiaecystid cornutes, defining a distinctive deep-water community associated with dysoxic substrates.

The NMDS ordination corroborates the clustering results by showing that assemblages belonging to the same faunal community plot close together in ordination space, while communities associated with contrasting environmental conditions are clearly separated (Fig. 10B). The main NMDS gradient separates shallow, high-energy shoreface communities from those living in deeper, offshore settings, although bathymetry alone does not significantly structure faunal composition (PERMANOVA, $p > 0.05$; see supplementary data). The second environmental control structuring these communities is bottom-water oxygenation, which significantly separates the dysoxic Landeyran assemblage from the two oxic assemblages (PERMANOVA, $p < 0.01$).

Differences between oxic and dysoxic offshore communities indicates that oxygen availability primarily acts as an ecological filter influencing body size, community abundance and structure (dominance patterns), rather than excluding entier taxonomic pools. Within the oxic realm, the gradual evolution of the relative sea level and of the associated environmental conditions (e.g. hydrodynamism) more likely affects both taxonomic richness and eveness, favoring abrupt taxonomic turnover.

Conclusions

The few determinations of trilobite species from the Cabrières material (i.e. *C. thorali*, *Geragnostus boutouryensis*) confirm the stratigraphical correlation with the lower part of the Landeyran Formation obtained from acritarchs (Caillaud *et al.* this volume). Although acritarchs, echinoderms and trilobites occupied completely different ecological niches, detailed analyses of their assemblages document very similar palaeoenvironmental trends in the lower part of the Landeyran Formation, contributing to a better understanding of the environmental context of the Cabrières Biota. Above the transition between the Foulon and Landeyran formations, marked changes in the composition of acritarch assemblages (decrease in galeates and *Michrystridium*, increase in baltisphaerids, taxa with complex processes, and veryhachids) suggest a clear transition from inner shelf, proximal environments to more distal, open shelf settings. The same transgressive trend is obvious with the shift from calymenid-dominated trilobite assemblages to more distal assemblages typical of the raphiophorid biofacies, and also with the shift from low-diversity eocrinoid-dominated meadows (upper part of the Cluse de l'Orb, and Foulon formations) to rare, but more diverse echinoderm assemblages dominated by cornutes (*A. incisus* Zone). Furthermore, the small size of echinoderms and the abundance of the mitrate *Lagynocystis pyramidalis* suggest the existence of dysoxic seafloor conditions. On the other hand, these dysoxic conditions do not modify the trilobite assemblages probably more tolerant to these conditions. These palaeoenvironmental interpretations based on acritarchs, trilobites and echinoderms are in perfect agreement with independently acquired data based on sedimentology, trace fossils, and the distribution of other fossil groups (e.g. conulariids). They all suggest that the Cabrières Biota inhabited poorly oxygenated soft substrates, in relatively distal, median shelf environments, below the storm wave base. However, these preliminary results need to be confirmed and further explored by geochemical elemental and isotopic data. They represent a first step for more complex ecological investigations, that will reconstruct community structure and assembly at a higher resolution and in a more computed and quantitative way.

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